ANIMAL SEED DISPERSAL AND ITS CONSEQUENCES FOR PLANT RECRUITMENT

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by

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"By creating the template for all subsequent population demographic processes, seed dispersal may provide a unifying theme for plant population ecology"

(Schupp and Fuentes, 1995)

TABLE OF CONTENTS

Abstract

Seed dispersal in New Zealand relies on a different guild from the one present before the arrival of humans into the islands. Post-dispersal biotic and abiotic filters have also changed due to the introduction of seed predators and herbivores. The aim of this thesis was to evaluate the actual contribution of seed dispersers to the patterns of seed fall and to understand the effects of biotic (seed density, predators, distance from conspecifics) and abiotic (pH, canopy openess, etc) factors on seed and seedling survival. I expected that tree species with different fruit sizes would be selected by different assemblages of dispersers, therefore being deposited and recruiting differentially on the forest floor.

I analyzed the changes in small-scale seed diversity with the use of seed traps during two seasons in two 0.36 ha plots in a mixed broadleaf-podocarp temperate forest. The diversity of seeds was lower for in-fruit seeds (1.40 species per grid-cell) than for bird-dispersed seeds (2.62). The dominant species *D. cupressinum* was dispersed towards con- and heterospecific canopies (wind-dispersed trees *Weinmannia racemosa* and *Metrosideros umbellata*), giving a probable mechanism for the observed increase in fine-scale seed diversity. Then, using a 12-year dataset on seed fall I analyzed the changes in ground-level seed heterogeneity generated by bird-dispersed seed rain (propagule-scale) relative to the canopy composition (adult-scale) on six tree species. A Non Metric Multidimensional Scaling analysis demonstrated that the differences in species composition between sampling points (seed traps) were larger for tree canopies than for dispersed seeds. Different tree species acted as seed importers and/or exporters, although these patterns were not explained by fruit size or the richness of the disperser assemblages.

I also investigated the effects of seed and seedling density on seed predation, seedling emergence and seedling survival to 12 months of five tree species. Seed predation increased with seed size, and it was higher at high density only for the largest-seeded species *Beilschmiedia tawa* and *Prumnopitys ferruginea*. Access of seed and seedling predators to the propagules was the main factor affecting seedling emergence and seedling survival. Abiotic variables were important for germination and seedling survival of the two small-seeded species, but only biotic predictors (mammalian exclosure and density) were important for medium and large-seeded species. Finally, using a split-plot experimental design I measured the effects of (a) the presence of conspecific canopy, (b) high conspecific seed densities and (c) introduced (or invasive) mammal access on seedling emergence and seedling survival (Janzen-Connell effects). Distance effects were stronger than density effects, and mediated by native and exotic predators. Final survival under conspecifics was strongly reduced in both species, with zero survival of *B. tawa* under conspecifics, and near zero (2/896) under *D. dacrydioides*.

Seed dispersal service in New Zealand is still enough to produce changes in the spatial pattern of seed deposition in the forest. Post-dispersal processes such as seed predation and herbivore are having strong impacts on the survival and potential recruitment of plant species. Large-seeded trees are the most affected in terms of the impact of introduced mammals on seed predation, but seedling survival is affected independent of seed size. However, it is unknown how different these ecological processes are from the original situation without pests in New Zealand. The results of my research can contribute with valuable information for future research trying to understand the consequences of seed dispersal for recruitment, as well as inform complex models that try to predict the long-term impacts of the exotic mammals introduced in New Zealand.

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Declaration of Contributions

Chapter 2: Frugivores enhance small-scale diversity in the seed rain of a mature temperate forest

Main author: Rocío C. Jaña

Contributors: Daniel García, Sarah J. Richardson and Dave Kelly

RCJ designed the experiment, searched the field sites, set up the experiment in the field, collected and sorted the samples, did the statistical analyses and wrote the manuscript. DK assisted with experimental design, DG helped with the theoretical background and focus of the chapter and reviewed all previous drafts of the chapter. DG, SJR and DK contributed to statistical advice. DK and SR reviewed the first and two last drafts.

Chapter 3: Biotic seed dispersal decreases seed rain heterogeneity in a mixed temperate forest

Main author: Rocío C. Jaña

Contributors: Sarah J. Richardson, Daniel García, Dave Kelly, Mick N. Clout, Brian J. Karl, Jocelyn Lewis and Jenny J. Ladley

MNC, BJK, JL, JJL and DK generated the12-year dataset RCJ used for this chapter (seed collection, seed identification and counting, and data entry). RCJ conceptualized the main hypotheses of the chapter, organized and analyzed the data, and wrote the manuscript. SJR, DG and DK assisted with statistical advice, helped to conceptualize the hypotheses of the chapter and reviewed all drafts of the manuscript.

Chapter 4: Effects of seed density and introduced mammals on seed survival, germination and survival

Main author: Rocío C. Jaña

Contributors: Sarah J. Richardson, Dave Kelly and Daniel García

RCJ designed, set and monitored the experiment in the field, analyzed the data and wrote the manuscript. DK and SR assisted with the statistical analysis and reviewed previous drafts. DG assisted with the methodology for seed predation experiment, reviewed the experimental design and the last draft.

Chapter 5: Janzen-Connell effects on two tree species in a temperate forest of New Zealand

Main author: Rocío C. Jaña

Contributors: Sarah J. Richardson, Dave Kelly and Daniel García

RCJ designed, set and monitored the experiment in the field, analyzed the data and wrote the manuscript. DK and SJR assisted with the experimental design, statistical analysis and reviewed previous drafts. DG reviewed the early experimental design and the last draft.

CHAPTER 1

Pseudopanax arboreus fruits

1 Introduction

1.1 The importance of seed dispersal and post-dispersal processes for plant recruitment

Seed dispersal is an important factor affecting the persistence and coexistence of plant species. In one way or another, a fraction of the reproductive structures are transported from the origin (parental individual) to a new microhabitat, where they will have the potential to germinate, grow and reproduce (Wang and Smith, 2002; Nathan et al., 2008). Furthermore, in community assembly, this propagule input is the hierarchically basal determinant of the progress of succession (Pickett et al., 1987). Some of the reported advantages of seed dispersal in plant populations are the avoidance of natural enemies or intraspecific interactions ("escape hypothesis") and the increase in the probability of finding a physically suitable establishment microsite ("colonization" and "directed dispersal" hypotheses) (Janzen, 1970; Connell, 1971; Howe et al., 1982; Willson and Traveset, 2000). If either of these mechanisms applies, dispersed propagules are more likely to survive to reproductive age than those that fall under the maternal plant (Howe and Miriti, 2004). The Janzen-Connell hypothesis proposes that seed dispersal is the main process responsible for the high-species diversity of tropical forests (Janzen, 1970; Connell, 1971; Wang and Smith, 2002). In their hypothesis, the areas that are closer to maternal trees will receive a higher seed rain than areas farther away, increasing the risk of species-specific density dependent mortality. Therefore, propagules will be more successful when they are in lower densities (more "scattered"), under heterospecific adults and/or away from parent trees, contributing to both population persistence and species coexistence (Kwit et al. 2007; but see Hubbell 1980). However, it is possible to find high seed densities away from the parent tree, under other conspecific and heterospecific adults, as a result of the behavior of the dispersal agent (Howe, 1989; Schupp and Fuentes, 1995; Clark et al., 2004). The consequences of these seed deposition patterns and its importance for plant population recruitment and community structure has not yet been fully addressed (Schupp, Milleron, & Russo 2002; Kwit et al. 2007; but see García, Martínez, & Obeso 2007).

In the case of animal-mediated seed dispersal, the efficiency of seed dispersal is dependent on the efficiency of the disperser guild (Schupp, 1993). The diverse structures around the seed, such as fleshy tissues, seed and fruit size, shape, weight, appendage structures (e.g. elaiosomes), together with other factors will determine the possible dispersal vectors of the propagule (dispersal syndrome) (Howe et al., 1982; Van der Pijl, 1982). In the case of endozoochory (seed dispersal via ingestion by animals) the seed

and/or fruit size and shape are two of the main determinants of the disperser guild. As seed size increases, the number of frugivores able to ingest them decreases due to physical constraints (Schupp, 1995; Forget et al., 2007). Consequently, species with large propagules will be dispersed by fewer organisms, narrowing the potential spectrum of dispersal agents. This is especially true for birds, where the differences in fruit size explains some of the differences in the guild of dispersers, as the gape width of the frugivorous birds is correlated with the range of ingested fruit sizes (Schupp, 1995; Herrera, 2002). Consequently, the dispersal vector, together with the characteristics of the parental individual and species (height, structure, distribution, etc) and the surrounding landscape structure, will determine the spatial distribution of the seeds coming from different plant sources (Willson and Traveset, 2000).

Even seed dispersal sets the template for future recruitment; post-dispersal processes shape the actual survival of seeds and seedlings. The microsite where a seed from a particular species will successful germinate is not necessarily the same microsite where a seedling will successfully survive (Cavallero et al., in press; Grubb, 1977; Schupp, 1995). The environmental (abiotic) filters acting post seed dispersal on plant regeneration can provide innumerable opportunities for differentiation, not only between species but also among individuals within a particular species (Clark et al., 2010). This process starts with the regeneration niche, which spans from seed dispersal to the establishment of the seedling or sapling (Grubb, 1977). Seed dispersal can vary in space and time, and seed survival will depend on its palatability and the presence and characteristics of the seed predators, as well as on the spatial and temporal variability of predation. Once the seed has survived, germination will subsequently be determined by some common (e.g. predators of seeds and seedlings, temporal variation in germination) and different factors from the ones determining seed survival, such as light availability, allelopathic effects, soil water contents, etc. This process continues until the seed has become a sapling (Grubb, 1977). Factors determining the transition of saplings to adult trees have also been investigated; however these work at different scales (Lusk and Smith, 1998; Wright, 2002; Coomes et al., 2005).

1.2 Seed dispersal and post-dispersal as spatially explicit processes

1.2.1 Seed dispersal

For endozoochorous species, the different frugivores consuming and dispersing the seeds will contribute in different ways to the different patterns of seed rain observed (Clark et al., 2005; Jordano et al., 2007). This generates a great variation in the diversity and quantity of seeds reaching different microsites, resulting in specific spatial distributions of seed rain for tree species that differ in the composition of their

dispersal assemblage, or have the same composition but differ in their attractiveness to the dispersers (Izhaki et al., 1991; Martínez et al., 2008). The physiology and behaviour of the disperser assemblage, including gut passage rate, habitat and foraging strata preferences, gregariousness, flight distances, rates of fruit removal, and perching and deposition sites and times will result in different seed deposition patterns for coexisting plant species, even with similar fruiting phenology and fruit characteristics (Dennis & Westcott 2007; Kwit et al. 2007; Martínez et al. 2008; Schupp et al. 2002 and references therein). The link between the identity of interacting plant-animal species and the consequent spatial post-dispersal seed deposition pattern still constitutes an open issue for research. However, in recent years, an increasing amount of research has been carried out comparing different seed dispersal patterns (seed rain, seed shadow or dispersal distances) generated by different dispersal vectors, e.g. primates and hornbills (Poulsen et al., 2002), birds, monkeys and wind (Clark et al., 2005), and birds and mammals (Jordano et al., 2007). In the same way, the number of studies comparing differential seed dispersal patterns resulting from different disperser assemblages within one group of dispersers is increasing (e.g. birds: Izhaki et al. 1991; Jordano & Schupp 2000; Jordano et al. 2007; Spiegel & Nathan 2007; Martínez et al. 2008).

The Janzen-Connell hypothesis is based on idealized smooth curves representing seed shadows as a function of distance from maternal plant, however, in his seminal work of 1970 Janzen pointed out the importance of the characteristics of the dispersal agent (smooth curves fit well mainly for wind dispersed species), and the spatial heterogeneity of the seed rain (Janzen, 1970; Schupp et al., 2002). The density of conspecific and heterospecific neighbors can influence seed deposition patterns too (the scale of the effect depending on disperser behaviour) by changing the removal rate of the focal species, reducing the dispersal distances of the seeds and influencing the intensity of post-dispersal seed predation, depending on the background species (Carlo, 2005; García et al., 2007; Carlo and Morales, 2008; Blendinger et al., 2011). Surprisingly, most research has focused on examining patterns of seed deposition and plant recruitment as a function of only the distance from the parental tree (or the nearest fruiting conspecific), without considering the interference of other elements (e.g. heterospecific adult trees) that might be concentrating high seed densities beneath them (but see Blendinger et al. 2011; Howe 1989; Kwit, Levey, & Greenberg 2004). Specific adult trees (conspecific or heterospecific) can be selected as roosting sites, latrines or perches concentrating seeds of diverse species beneath their canopy (Schupp et al., 2002; Kwit et al., 2004, 2007), or concentrating seeds from simultaneously fruiting species with a shared disperser assemblage (Clark et al., 2004).

1.2.2 Post-dispersal

After seed dispersal by the different agents involved (animals, wind, water) different mechanisms will act to control what species will succeed in recruiting to the adult stage. Diverse hypotheses have been

postulated to explain the actual species diversity in forests, particularly in tropical forests (Chesson, 2000; Wright, 2002; Clark et al., 2010). Density-dependence influenced by the proximity of conspecifics (Janzen, 1970; Connell, 1971) is one of the most frequently tested hypotheses (Hyatt et al., 2003; Carson et al., 2008; Terborgh, 2012). Niche differentiation through environmental filters (Grubb, 1977) from the seed to the adult stage has also found wide support (Clark et al. 2010; Coomes 2003; Schupp & Fuentes 1995; Silvertown 2004; among others).

Density-dependent processes, however, can act not only in the proximity of conspecifics, but also in the proximity of other feeding sources or sites preferred by the potential predators (soil pathogens, invertebrate and vertebrate animals) (Janzen, 1970, 1971; Connell, 1971). The mechanisms involved are allelopathy (when seeds/seedlings are near conspecifics), intraspecific competition and attraction or facilitation of attacks by pathogens and/or predators. Natural enemies in conjunction with the distance from conspecifics have been indicated as the main drivers for tropical forest's tree diversity, reducing the survival of seeds and seedlings near conspecifics (Terborgh, 2012). However, Clark et al. (2012) in a lowland tropical forest at the Republic of Congo found that seed predators and herbivores were the main drivers reducing seedling emergence and seedling survival of five tree species, and that distance to conspecifics was not the main predictor involved. However, for other species, seed density can be determinant of their survival, and will interact with the different types of seed predators (vertebrates, invertebrates or soil pathogens) and the distance from conspecifics (Wotton and Kelly, 2011; Beckman et al., 2012). The effects of conspecifics and seed density on seed and seedling survival are often species-specific, context-dependent, and it is difficult to generalize the results towards a complete community or forest type (Hyatt et al., 2003; Carson et al., 2008; Terborgh, 2012).

1.3 The present state of seed dispersal, seed and seedling predation in New Zealand

Temperate forests present moderate proportions of fleshy-fruited species, compared to tropical forests (Willson, 1991). In New Zealand forests, in particular, the 59% of the trees and the 31% of the basal area covered by forests are bird-dispersed plants (Thorsen et al., 2009; Kelly et al., 2010).

1.3.1 Seed dispersers

It is widely known that the avifauna of New Zealand has gone through a major reduction since the arrival of humans (Maori people 800 years ago, and Europeans in 1840; Atkinson & Cameron 1993; Wilson 2004). In particular, the lack of terrestrial mammals left birds, two bat species, and reptiles as the vertebrates primarily responsible for all animal seed dispersal (Whitaker, 1987; Clout and Hay, 1989;

Wotton, 2002; Kelly et al., 2006). In the pre-human New Zealand avian seed dispersers are though were probably two moa species (*Eutyapteryx spp*.), huia (*Heteralocha acutirostris*), piopio (*Turnagra capensis*) (all four species now extinct), whitehead (*Mohoua albicilla*), kokako (*Callaeas cinerea*), saddleback (*Philesturnus carunculatus*), hihi (*Notiomystis cincta*), New Zealand pigeon (*Hemiphaga novaeseelandiae*), tui (*Prosthemadera novaeseelandiae*), bellbird (*Anthornis melanura*), weka and brown kiwi (the two latter are ground foragers; *Gallirallus australis* and *Apterix australis*, respectively) (Holdaway, 1989; Atkinson and Millener, 1991). The greater short-tailed bat (*Mystacina robusta*, now extinct) and the lesser short-tailed bat (*M. tuberculata*) were consumers of small fruits (Daniel, 1976; Lloyd, 2005). New Zealand had also a large diversity of geckos and skinks, some of them thought to have consumed fruits from shrubs, although probably transporting the seeds only short distances (Whitaker, 1987; Lord et al., 2002; Wotton, 2002). Invertebrates such as wetas (Orthoptera) can also disperse seeds, however their home ranges are small (depositing seed very close to the source, frequently on the same tree) and most of the seeds are destroyed during gut passage (Duthie et al., 2006; Morgan-Richards et al., 2008; Wyman et al., 2011).

However, today's disperser assemblages are quite distinct to those from the past. Overall, 45% of all the native bird species have disappeared from the mainland (Holdaway, 1989; Wilson, 2004; Anderson et al., 2006). Of the seed dispersers, only the New Zealand pigeon, tui and bellbird are still widespread enough in the mainland to constitute important seed dispersers (Anderson et al., 2006; Kelly et al., 2006, 2010). Although the populations of these species were reduced with the arrival of humans they are currently recovering after pest-control programs and species-specific research (Innes et al., 2010).Together with the silvereye (*Zosterops lateralis*, a small self-introduced species from Australia), these species can constitute up to 84% of all bird fruit removal observations in a given site (Kelly et al., 2006). Also new bird species acting as seed dispersers (Beveridge, 1964; O'Donnell and Dilks, 1994; Burns, in press) are now present in New Zealand forests: song thrush (*Turdus philomelos*), blackbird (*T. merula*) and starling (*Sturnus vulgaris*). Unpublished records show that the diet of these last three species can be composed of up to 83% seeds from native species, however the diversity of native plants they forage on is reduced (A. MacFarlane unpublished data). Regarding the mammals, the greater short-tailed bat is now extinct, and the lesser short-tailed bat has a very restricted distribution on the mainland so its function as a seed disperser is minimal (Lord et al., 2002; King, 2005). Brushtail possums (*Trichosurus vulpecula*) are now present all through the mainland, consume fruits from many species but are able to disperse only a small fraction of seeds, and only those smaller than 10 mm (Williams et al., 2000; Dungan and Norton, 2003; Williams, 2003). Gecko and skink populations have been also reduced, and several species are extinct on the mainland (geckos: 4 of 32 species; skinks: 13 of 32 species; Wilson, 2004)),

however their role as seed dispersers is limited mainly to dense shrubs (Lord et al., 2002; Wilson, 2004). Seed dispersal service in current New Zealand is likely to be reduced compared to the pre-human situation, however, the contribution of the exotic species (birds, possums) is still controversial and not studied enough (O'Donnell and Dilks, 1994; Williams et al., 2000; Dungan and Norton, 2003; Williams, 2003; Kelly et al., 2010; Burns, in press).

1.3.2 Post-dispersal seed predators and ground herbivores

Not much information is available on what species acted as post dispersal seed predators before the arrival of humans; however, it is thought that it was mainly based on birds and invertebrates. Potential seed and seedling predators are the ground foragers that consumed plant material as moas (several species), takahe (*Porphyrio hochstetteri*), kakapo (*Strigops habroptilus*), Finsch's duck (*Euryanas finschi*), red-crowned parakeet (*Cyanorampus novaeselandiae*) and brown kiwi (Reid et al., 1982; Holdaway, 1989; Atkinson and Millener, 1991; Wilson, 2004). Kereru and kokako are unlikely to have predated seeds, as they act as seed dispersers, but they fed on plant material on the ground (Clout and Hay, 1989; Atkinson and Millener, 1991). Little is known about invertebrate post-dispersal seed predators before the mammalian invasions. In previous times wetas used to be abundant species in the mainland (Wilson, 2004), and these act a seed predators (and occasionally as seed dispersers) on trees and on the ground (Duthie et al., 2006; Morgan-Richards et al., 2008; Wyman et al., 2011).

Today the seed predator assemblage has dramatically changed. Most of the ground foragers from the past are now extinct (moas, Finsch's duck) or with very restricted distribution (takahe, kakapo, kokako, brown kiwi, red-crowned parakeet), mainly surviving only in predator-free reserves (Greene, 1998; Wilson, 2004; Robertson et al., 2007). Even though wetas (and probably most of the invertebrate species) are still present on the mainland, their populations have been heavily reduced as they are prominent in the diet of ship rats (*Rattus rattus*), the most widespread introduced rodent in New Zealand (King, 2005). Dramatic increases in weta numbers have been detected in a sanctuary after excluding all mammalian pests (Watts et al., 2011). Weta are also able to change their behaviour in the presence of mammalian predators (Bremner et al., 1989), even travelling longer distances and using cavities closer to the ground four years after the erradication of mammals and weka (Rufaut and Gibbs, 2003). This certainly would have consequences on their feeding behaviour if they used to feed on fallen fruits or seeds on the ground. The main group of post-dispersal seed predators and seedling herbivores in forests are today the introduced mammals (Beveridge, 1964; Campbell, 1978; Berry, 2006). Ship rats and possums feed on the forest floor, and eat seeds and seedlings from a variety of species (Beveridge, 1964; Beveridge and Daniel, 1965; Campbell, 1978; Grant-Hoffman and Barboza, 2010). House mice (*Mus musculus*) consume important proportions of seeds, especially after masting events (Ruscoe et al., 2004;

McQueen and Lawrence, 2008). Important reductions on seedling numbers are attributed to rats or possum, depending on which species is more abundant (Wilson et al., 2003). Although one study (Moles and Drake, 1999) reported low rates of seed predation, others with more spatial and temporal replicates, and followed for longer periods have found strong effects on rodents and possums on seed and seedling survival (Beveridge, 1964; Wilson et al., 2003; Berry, 2006; Wotton and Kelly, 2011).

1.4 Thesis outline

In this thesis I used the link between seed size and the disperser assemblage to try to understand the seed deposition patterns in two temperate forests in New Zealand. Then, as I expected dispersers to change the aggregation levels and the species composition of the seed rain, I studied the effects of: (1) seed density, (2) access of introduced mammals and (3) distance to conspecifics on seed predation, seedling emergence and survival, still in the context of seed size. I developed these specific points through four data chapters and one final chapter of synthesis. Because each chapter has been written in a suitable format for submission to a journal, Figures and Tables are numbered within each chapter, and appendices are included at the end of that chapter.

Seed deposition patterns are dependent on the foraging behaviour of the dispersers as well as the fruiting community were they feed on (Nathan and Muller-Landau, 2000; Morales and Carlo, 2006; Blendinger et al., 2011). There is inter-specific and intra-specific variation in the fruiting patterns of trees, and dispersers base their food selection on the characteristics of the trees (fruit size, crop size) and fruits (nutritional contents) they feed on (Carlo, 2005; Carlo and Morales, 2008). Seeds can be deposited more often under conspecific canopies generating positive spatial feedback into the community, or can be transferred between heterospecific canopies, increasing seed diversity at ground level (Clark et al., 2004; Kwit et al., 2004; García et al., 2007) (Chapter 2). When seeds are transferred between heterospecific canopies, the similarity between the seed rain under the canopy of fruiting trees is increased, with trees along a gradient of conspecific/heterospecific seed rain under its canopy (Herrera et al., 1994; García et al., 2007) (Chapter 3).

The fate of seeds and seedlings from dispersed seeds is dependent on biotic and abiotic factors, which will determine differential survival in the forest floor (Clark et al., 2012). Seed density and predation can shape the survival curve for the different species with different seed sizes (Janzen, 1970, 1971; Connell, 1971), but this will be also determined by environmental factors such as pH, canopy opening, and the amount of organic soil, among others (Grubb, 1977; Silvertown, 2004) (Chapter 4). The presence of conspecific canopy above the seeds can also affect differential survival for seeds on the

ground, mediated by seed density and host-specific predators as soil pathogens, invertebrates and vertebrates (Janzen, 1970; Connell, 1971) (Chapter 5). The final chapter synthesizes the findings of my research, analyzing the current state of knowledge of these processes mainly in New Zealand, and highlights the areas where more research would be welcomed.

CHAPTER 2

Seed trap in Okarito Forest, South Island, New Zealand

2 Frugivores enhance small-scale diversity in the seed rain of a mature temperate forest

2.1 Abstract

Dispersers can modify the species diversity on the ground at a local scale. We identify the possible mechanisms for this and try to distinguish some of them. We use the seed transfer between heterospecific canopies and seed rain under conspecifics as the two basic mechanisms that can modify the combination of plant species in the seed bank through seed dispersal. Can seed dispersers modify the local diversity, generating new combinations of seeds through the process of seed dispersal?

With the use of seed traps we collected seed rain from mapped trees and shrubs during two seasons, March to September 2009 and January to September 2010, in two 0.36 ha plots in a mixed broadleaf-podocarp temperate forest, Westland, South Island of New Zealand. We classified the seeds in two different categories: in-fruit seeds as a surrogate of pre-dispersal situation, and bird-dispersed seeds. We then analyzed the level of aggregation of both, and its spatial association with the adult trees in the plots.

The dominant species *Dacrydium cupressinum* dominated the seed rain in both seasons. The inverted Simpson's index for the diversity of seeds was lower for in-fruit seeds (1.40 species per grid-cell) than for bird-dispersed seeds (2.62) and post-dispersal (intact + in-fruit) seed diversity (2.03). Seed diversity of bird-dispersed seeds tended to be more associated to tree diversity than in-fruit seeds diversity, however none of the association indexes were statistically significant.. The dominant species *D. cupressinum* was dispersed towards con- and heterospecific canopies, giving a probable mechanism for the observed increase in fine-scale seed diversity through the presence of balanced spatial positive feedback (SPF) and heterospecific seed transfer (HST). Two wind-dispersed trees were associated to *D. cuppressinum* dispersed seeds, probably offering an alternative food source for the dispersers (e.g. nectar or insects). Therefore, seed dispersers increase the local or small-scale diversity through seed dispersal however, seeds were not dispersed towards particular tree species in the plots.

2.2 Introduction

Seed dispersers have the capacity to modify the combination of species in the propagule bank through movements of seeds in the landscape (Clark et al., 2004; García et al., 2007), "sowing" the potential for changes in the community composition and structure (Schupp and Fuentes, 1995). These changes can

occur at small or large scales, with consequences for the community such as shifts in the relative abundance of species, arrival of new species or simply increases or decreases in the level of aggregation of the existing species (Clark et al., 2004; Kwit et al., 2004, 2007). Specifically, it can determine the spatial distribution of different plant species and underpin their coexistence (Seidler and Plotkin, 2006; Hampe et al., 2008).

Spatial patterns of seed dispersal are strongly determined by the interaction of the local frugivore community with plant traits influencing frugivore selection and behaviour (Schupp et al., 2002; Muller-Landau et al., 2008). Fruit crop, plant height, crown architecture, seed and fruit traits, and the dispersal syndrome are some of the plant traits that affect the deposition of seeds (Clark et al., 2004; Kwit et al., 2007; Muller-Landau et al., 2008; Lin et al., 2011). All these elements determine the probability of seeds reaching con- or hetero-specific canopies in the community. The frugivores can modify the combination of species in the propagules bank through heterospecific seed transfer (HST onwards, García *et al.* 2007). HST consists in the movement of seeds from a source canopy to areas beneath heterospecific canopies (e.g. spatially contagious seed dispersal, Kwit, Levey, & Greenberg 2004; García *et al.* 2007), therefore having the potential to change the community structure. It can be generated by the use of sleeping sites by mammals, perching preferences by birds, roosts, nest locations and latrines, and more generally by the use of heterospecific fruiting trees (Debussche and Isenmann, 1994; Clark et al., 2004; Kwit et al., 2004; Russo and Augspurger, 2004; García et al., 2007; White and Vivian-Smith, 2011). Seed transfer between heterospecific canopies can also occur at a local scale (local HST) or between canopies far apart from each other (long-distance HST). In addition to HST, frugivores can also generate a spatial positive feedback in the seed rain (SPF onwards) by depositing seeds under the canopy of the parent or under conspecific canopies, thus maintaining and reinforcing the community composition and structure.

The balance between the processes of heterospecific seed transfer (HST) and spatial positive feedback (SPF) will determine the level of increase in post-dispersal seed diversity relative to seed diversity in the canopy. If animal mediated seed dispersal is not strong enough to change the patterns of seed deposition for the different species, then we would not expect a change in ground-level seed diversity. If seed dispersers are transferring seeds between heterospecific canopies, therefore increasing HST, and at the same time, reducing SPF, then we would expect to detect an increase in seed diversity at ground level when comparing pre-dispersal seed diversity against post-dispersal seed diversity. To understand how HST and SPF can affect ground level seed diversity it is necessary to analyze the spatial association between the seed fall patterns of the different animal-dispersed plant species and the respective con- and heterospecific adults present in the community. In the case of species whose seed fall

is biased towards heterospecific canopies, these species would be increasing the HST and therefore, the ground level seed diversity.

We analyze post-dispersal seed fall patterns in a low-diversity temperate forest of New Zealand and evaluate its spatial associations with con- and hetero-specific trees. We categorized seed rain in terms of bird-dispersed versus in-fruit seeds. We use in-fruit seeds as a surrogate of the pre-dispersal situation, where seeds falling from canopies are expected to be strongly aggregated under the parent tree, and inserted in less diverse clumps than in-fruit seeds in the post-dispersal situation. The ideal system to test my hypothesis of the effect of animal-mediated seed dispersal on HST and SPF would be constituted by the comparison of seed deposition patterns with and without seed dispersers. However, this is impracticable in studies with a community approach as the one we present here (but see Aukema & Martínez del Rio 2002). We therefore used the comparison between bird-dispersed seeds and in-fruit seeds as a resemblance of seed fall with and without seed dispersers. My aim is to identify the occurrence of HST and SPF as a possible mechanism that could explain the increase in diversity, and to disentangle the pathways in seed dispersal that could modulate it. We expect an increase in seed diversity through animal-mediated seed dispersal and, with the use the dominant species of the studied community we analyze the mechanisms that may explain seed diversity patterns. We evaluated the following specific question: Are the dispersers modifying the small-scale propagule diversity on the ground, generating new "starters" of seed combinations for the community succession? If yes, can we identify possible mechanisms for this?

2.3 Methods

2.3.1 Study species and sites

The study was conducted in North Okarito Forest (8 760 ha), an extensive old-growth coastal podocarp-broadleaf forest situated in Westland, New Zealand (43°20' S, 170°30' E, 50 m.a.s.l.). The annual rainfall is approximately 3400 mm, evenly distributed during the year. Mean annual temperature is 11.3°C, with a daily average temperature in winter of 7.0 °C and summer 15.2 °C (Whitehead et al., 2002). The forest is established on terrace outwashes from morraines formed approximately 20 000 years ago, therefore the topography is mainly flat (Turnbull et al., 2003). The forest is dominated by a large (mean height 20 m), emergent conifer *Dacrydium cupressinum* (Podocarpaceae), accompanied in the subcanopy by *Prumnopitys ferruginea* (Podocarpaceae) and *Weinmannia racemosa* (Cunoniaceae). Other subcanopy but less common species are *Metrosideros umbellata* (Myrtaceae), *Quintinia acutifolia* (Paracryphiaceae), *Manoao colensoi* (Podocarpaceae) and *Podocarpus hallii* (Podocarpaceae)(James and Norton, 2002;

Turnbull et al., 2003). The understorey is dominated by *Griselinia littoralis* (Griselinaceae) trees, shrubs as *Neomyrtus pedunculata* (Myrtaceae), *Myrsine divaricata* (Myrtaceae) and a large variety of *Coprosma* (Rubiaceae) species. All these species except *W. racemosa*, *M. umbellata*, and *Q. acutifolia* are fleshy-fruited.

The dominant species in Okarito Forest, *D. cupressinum* is a dioecious tree, a quite frequent feature of New Zealand flora (Webb and Kelly, 1993). Male:female ratio of individual trees in terrace forests of New Zealand has been found to be 51:49 (Foweraker 1932 in Norton, Herbert, & Beveridge 1988). *Dacrydium* presents a small arilated oblong-seed (fruit hereafter, Table 1), and its crop size is highly variable between years (Norton and Kelly, 1988). This species comprises 67% of the total tree basal area in the study site (Table 1).

Regarding to the dispersers of seeds of woody plants, nine frugivorous/omnivorous bird species have been recorded in the zone in previous years by Spurr et al. (1992). The most common is *Anthornis melanura* (Meliphagidae), followed by *Zosterops lateralis* (Zosteropidae), *Hemiphaga novaeseelandiae* (Columbidae), *Prosthemadera novaeseelandiae* (Meliphagidae) and *Turdus merula* (Turdidae) All but *Turdus* are native species. There are no native mammalian dispersers at my study site (Lloyd, 2005).

2.3.2 Experimental plots

We established two 1 hectare plots (100 x 100 m each) located 2 km apart, in un-logged areas of Okarito Forest. Each plot was divided into one-hundred 10 x 10 m cells, and all the trees larger than 10 cm dbh were mapped to the nearest 10 cm. Seed traps were placed in the central 60 x 60 m (36 cells), and all the statistical analyses were based in these sub-section of the plots.

Seed rain was collected using seed traps during two consecutive fruiting seasons. Four seed traps (26 cm diameter each) were evenly distributed within each cell. Seed traps consisted of plastic buckets with drainage holes fixed to the ground with a metal peg. A thin mesh bag suspended at least 10 cm above the bottom of the container was placed in each seed trap to capture all seeds larger than 2 mm, and to let the water drain. Because of the large size of some fruits in the forest (e.g. *P. ferruginea,* fruit 12.7-13.2 mm wide) no covering was placed on top of seed traps, as these could bounce on it reducing the number of seeds captured in the seed trap. Mammal faeces or evidence of them were never found inside seed traps. Only *D. cupressinum* seeds were found eaten inside of seed traps, however, this species has been previously reported as being heavily consumed (near 80% of fruit crop) in the canopy, mainly by ship rat (*Rattus rattus*) and probably finches (Beveridge, 1964). Other seeds as *P. ferruginea* often found consumed on the forest floor at the study site (R.C.J. personal observation) were found intact inside the seed traps. On three occasions during the two seasons, a seed trap was found knocked over, presumably by mammal activity. In these cases, the seed trap contents were excluded from the analysis.

In the study sites most of the plants in the area bear ripe fruits during autumn and winter (O'Donnell and Dilks, 1994). In the first season, sampling was carried out from March to beginning of September 2009 (n = 144 seed traps per plot). In the second season to increase the catch, one extra seed trap was placed in each cell and the time span was extended (second season: January - September 2010, n = 180 seed traps per plot). All seeds larger than 2 mm long or wide were identified to species level (except for some *Coprosma* species, identified as morphospecies) using on-site fruit collection, reference books and the seed collection from the Allan Herbarium at Landcare Research (Lincoln, Canterbury). Seeds from animal droppings that act as dispersers are intact and free of fruit pulp, so they can be easily identified as animal- dispersed. As birds are the main seed disperser guild in the sites and no mammal faeces were found inside the buckets, animal-dispersed seeds in my study are assumed to have been consumed by birds. All seeds from fleshy-fruited species found in the seed traps were separated, and classified as: bird-dispersed seeds, damaged seeds (partly destroyed or fragmented by a seed predator or granivore) or in-fruit seeds (seeds inside fruits). Only un-damaged and ripe seeds were considered in the analyses, as attacked and unripe seeds are generally not viable.

2.3.3 Statistical analyses

The purpose of this study is to identify the occurrence of HST and SPF, quantifying the effects of animal-mediated seed dispersal in ground-level seed diversity, and identifying the possible mechanisms that could generate this pattern. To do this I first evaluated seed diversity at ground level in terms of in-fruit seeds and bird-dispersed seeds. I then calculated the levels of spatial aggregation in the seed rain, basal areas of the trees and the spatial association between them. I finally used the information for the dominant tree and seed species, *D. cupressinum*, to quantify the balance between HST and SPF, analyzing its seed fall patterns, and its association with con-specific and heterospecific trees in the plots.

To improve seed numbers for the analyses all seed traps per cell (n = 4 first season, n = 5 second season) and the two sampling seasons were pooled, and analyses run at the cell (10 m x 10 m) scale. I consider that as seed numbers were uniformly low across the two sampling seasons, and did not vary intra-specifically between years this decision will not affect the results. All diversity analyses were based on the inverted Simpson's index, because of its robustness against variation in sampling effort and its utility when it comes to compare diversity between communities (Magurran, 2004).

To test for the general effects of biotic seed dispersal on seed abundance and diversity, I fitted linear mixed-effects models (LMM, Pinheiro & Bates 2000) to the data, using the "nlme" package in R version 2.13.1 (R Development Core Team, 2011). I considered seed type (categorical: bird-dispersed or in-fruit seeds) as a fixed factor, plot as a random factor and seed diversity or seed abundance as response variables. Model parameters were fitted by restricted maximum likelihood (REML). I also tested for

changes in seed diversity at cell level between in-fruit seed diversity and overall seed diversity (in-fruit + bird-dispersed), using a paired t-test.

I used the Spatial Analysis by Distance Indices technique (SADIE, Perry et al. 1999; Perry & Dixon 2002) to analyze the spatial patterns of seed deposition and its association with basal areas of trees. This technique was developed for the analysis of ecological data in the form of spatially referenced counts, and it has the advantage over other spatial analyses that its output can be visualized as contour plots, allowing the identification of clusters and gaps in the space. SADIE was initially designed to detect spatial patterns in the form of clusters, either patches or gaps, giving an index of overall aggregation I_a. It is based on the distance that counts in the observed data need to move to generate a regular distribution in the space, with equal abundances in each cell, relative to the distance calculated from randon permutations of the data (Perry et al., 1999). Values of $I_a > 1$ indicate aggregation of observed counts into clusters, $I_a = 1$ indicates randomly arranged counts, and $I_a < 1$ regular distributions (Perry et al., 1999). SADIE also calculates an index of local clustering v for each cell-count. An extension of SADIE was developed to assess similarity between the spatial disposition of clusters (patches and gaps) belonging to two datasets, on the base of correlation between the clustering indices v (Winder et al. 2001; Perry & Dixon 2002). From these correlations an index of association between each pair of cells is calculated, X_i, and from it, an overall association index X_p. This X_p is similar to the aggregation index I_a in that X_p values larger than 1 indicate a positive association between the clusters of both datasets, $X_p = 0$ no association nor dissociation, and $X_p < 1$ complete dissociation. Critical values for the association analysis are automatically corrected for autocorrelation using the Dutilleul method (Perry and Dixon, 2002). Both aggregation and association analyses are statistically tested by randomization tests. SADIE analyses were conducted with the software Sadie Shell v1.22 (Conrad, 2001).

I ran the spatial analyses for collected seeds (seed species diversity and *D. cupressinum* abundance), trees species diversity (all species, fleshy fruited species and wind dispersed species) and trees abundances of the commonest species (same as diversity plus *D. cupressinum*, *P. ferruginea*, *W. racemosa*, *M. umbellata* and *Q. acutifolia*). The first step for the analysis is to run aggregation analyses on all the variables of interest (Table 2), and second, the information obtained is used to estimate the spatial association between pairs of variables of interest. The association analysis is run using paired correlations between the local clustering indexes v of each of the two datasets. I analyzed the possible mechanisms that can explain the change in seed diversity. I first tested if seed diversity was more closely associated to the diversity of trees in the plot after dispersal, through the analysis of the spatial association between seeds diversity and trees diversity, for in-fruit seeds and bird-dispersed seeds (diversity of seeds and diversity of all trees, diversity of seeds and diversity of fleshy fruited trees, diversity of seeds and

diversity of wind dispersed trees). I then studied the balance between HST and SPF using the seed deposition patterns of the dominant species *D. cupressinum* as a model and its association with the abundance (in terms of basal areas) of the different groups of trees (i.e dispersal syndromes and species: all trees, fleshy fruited, wind dispersed, *D. cupressinum*, *P. ferruginea*, *W. racemosa*, *M. umbellata* and *Q. acutifolia*) in the plots (Table 3).

Finally to test the statistical significance of the changes in the spatial association of *D. cupressinum* seeds and the trees in the plots I ran an ANOVA with *Xp* as the response variable, tree group (see above), seed type (in-fruit vs. bird-dispersed), and plot as predictors.

2.4 Results

Both plots were similar in the composition (total and relative abundances, species richness) of plant community, both at the stage of adult trees and the seed rain (Table 1). A total of 3 694 seeds were collected during the two seasons, 47% of them were bird-dispersed. I found seeds from 41 vascular plant taxa in the plots. All seeds were identified at species level, except for some *Coprosma* spp identified as morphospecies. *Dacrydium cupressinum* was the dominant species in terms of basal area of the plots (67%) and seed rain (68%). Five tree species accounted for 97% of the total basal area (Table 1).
The proportion of bird-dispersed seeds, relative to the total number of seeds collected in the seed traps was highly variable between species (e.g. *Myrsine divaricata* and *Ascarina lucida*), but similar within species between plots (Table 1). Approximately one third of *D. cupressinum*, and all of *Coprosma parviflora* and *Nertera depressa* seeds were collected as bird-dispersed seeds.

2.4.1 Change in seed diversity

Seed diversity was higher for bird-dispersed seeds than for in-fruit seeds (GLM, mean bird-dispersed = 2.62 species per cell, mean in-fruit = 1.40, $F_{1,141} = 62.309$, $P<0.0001$). To compare the net change in the diversity at cell–level I also compared in-fruit seed diversity against all seeds diversity (bird-dispersed plus in-fruit seeds). Diversity of all collected seeds was higher (paired t-test, $t = -8.56$, df = 71, $P<0.0001$; Fig. 1). Local seed-rain abundance was not affected by the seed type (mean bird-dispersed = 24.1 seeds per cell, in-fruit = 27.2, $F_{1,141} = 1.166$, $P = 0.28$).

Table 1. Dominant species in the seed rain and their key dispersal traits in Okarito Forest, New Zealand. Seed rain was sampled in two 1 ha plots from March to September 2009, and January to September 2010. Estimates of basal area are based on all stems with a diameter at breast height (dbh) ≥ 10 cm. The % of total basal area is shown for species dominant in the seed rain (those that cumulatively account for at least 95% of all seeds collected). NA indicates wind-dispersed species for which seed rain was not quantified, + represents species present but with no stems > 10 cm dbh, ~ represents approximate values for plant traits. References are †Allan 1961, ‡Webb & Simpson 2001, ¶Kelly et al. 2010, §J. Lord unpubl. data.

Plant species	Family	Plant height† (m)	Fruit diameter† (mm)	Seed length‡ (mm)	Seed diameter‡ (mm)	% of total basal area (stems per plot)		Seed rain (% bird-dispersed)	
						Plot 1	Plot 2	Plot 1	Plot 2
Bird-dispersed species									
Dacrydium cuppressinum	Podocarpaceae	35	~2	3.2–3.8	~2	67.3 (162)	67.8 (126)	1307 (33.7)	1205 (34.4)
Prumnopitys ferruginea	Podocarpaceae	25	13 ¶	11–17	~10	8.4 (60)	5.9 (21)	7 (71.4)	33 (90.9)
Griselinia littoralis	Griseliniaceae	15	4 §	5–6	~3.5	0.34 (11)	0.53 (9)	26 (73.1)	39 (61.5)
Phyllocladus alpinus	Phyllocladaceae	9	cone	2.5–2.9	~1.6	0.03 (2)	+	35 (74.3)	7 (85.7)
Neomyrtus pedunculata	Myrtaceae	6	~6	~2.5	2.0–2.5	+	+	196 (80.1)	57 (100)
Ascarina lucida	Chloranthaceae	6	1.8 §	1.3–2.0	~1.2	0.13 (4)	0.36 (11)	26 (38.5)	240 (37.5)
Coprosma parviflora	Rubiaceae	5	5	2.3–3.3	2.2–2.8	+	+	4 (100)	36 (100)
Myrsine divaricata	Primulaceae	3	4–5	2.5–3.50	2.3–3.1	+	+	44 (95.5)	118 (91.5)
Nertera sp. *(depressa?)*	Rubiaceae	<0.3 (herb)	4	~1.2	1.7–2.4	+	+	64 (100)	36 (100)
Ripogonum scandens	Ripogonaceae	Liana	10	7.01	7.80	+	+	41 (39)	8 (62.5)
Wind-dispersed species									
Weinmannia racemosa	Cunoniaceae	25				11.6 (309)	22.6 (650)	NA	NA
Metrosideros umbellata	Myrtaceae	15				8.2 (13)	Absent	NA	NA
Quintinia acutifolia	Escalloniaceae	12				2.4 (55)	1.4 (11)	NA	NA
Total	–	–	–		–	61.8 $m^2 \cdot ha^{-1}$	59.5 $m^2 \cdot ha^{-1}$	1811 (46.1)	1883 (47.8)
Number of species	–	–	–		–	15	14		

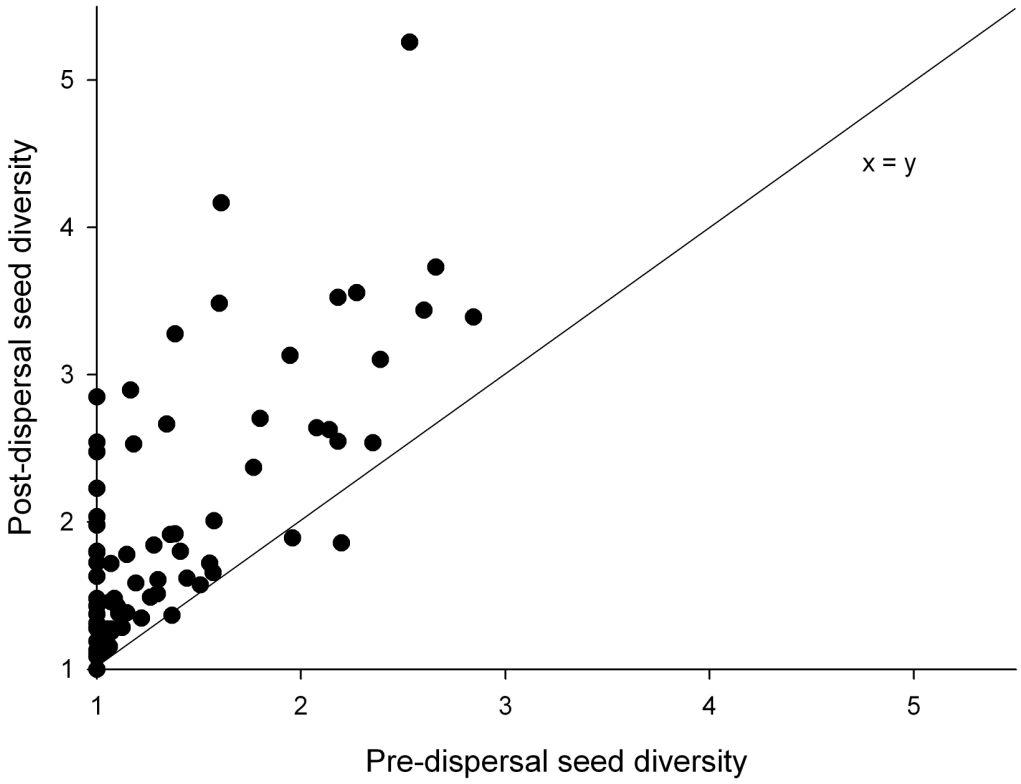


Figure 1. Changes in pre- (in-fruit seeds) and post-dispersal (all seeds) seed diversity per cell. All seeds collected, independent of the habit growth of the plant species, were used.

2.4.2 Spatial associations between seeds and trees

Seed fall and basal area were generally not significantly aggregated (Table 2). In-fruit seed diversity was significantly aggregated in Plot 2. However, the diversity of wind-dispersed trees was aggregated in Plot 1.

The association between seed and tree diversity was non-significant all cases (Table 3). However, the value of the non-significant association index between the diversity of seeds and diversity of trees for bird-dispersed seeds was higher compared to in-fruit seeds, for all groups of interest: all the trees, fleshy-fruited trees and wind-dispersed trees (Table 3, Fig. 2).

The patterns of association between *D.cupressinum* seeds and different groups of trees differed between plots (Table 3). *D. cupressinum* bird-dispersed seeds were associated significantly to the abundance of trees, and more specifically, to the abundance of wind-dispersed trees in Plot 1 but not in Plot 2 (e.g. Fig. 3). There was, however, a tendency for a higher association of *D. cupressinum* seeds with all trees, fleshy-fruited trees and wind-dispersed trees across the two plots through seed dispersal.

Table 2. Values of the index of aggregation (*Ia*) provided by SADIE for seed rain abundance and diversity for two seed types (bird-dispersed cf. in-fruit seeds) and for tree basal area. Indices indicating a significant ($P \leq 0.05$; i.e. non-random) spatial aggregation are marked with asterisks (* $P < 0.05$, ** $P < 0.01$).

Parameter	Seed or basal area type	Plot 1	Plot 2
(1) Seed diversity	All in-fruit	1.034	1.511**
	All bird-dispersed	1.154	1.204
(2) Seed abundance	*D. cupressinum* in fruit	1.223	0.980
	D. cupressinum bird-dispersed	1.167	1.184
(3) Basal area diversity	All	1.276	1.119
	Fleshy fruited	1.317	0.983
	Wind-dispersed	1.372*	0.931
(4) Basal area abundance	All	1.220	0.921
	Fleshy fruited	1.075	0.839
	Wind-dispersed	1.293	0.999
(5) Single species basal area	*Dacrydium cupressinum*	1.129	0.822
	Prumnopitys ferruginea	0.845	0.880
	Weinmannia racemosa	1.199	0.819
	Metrosideros umbellata	1.008	Species absent
	Quintinia acutifolia	0.933	1.153

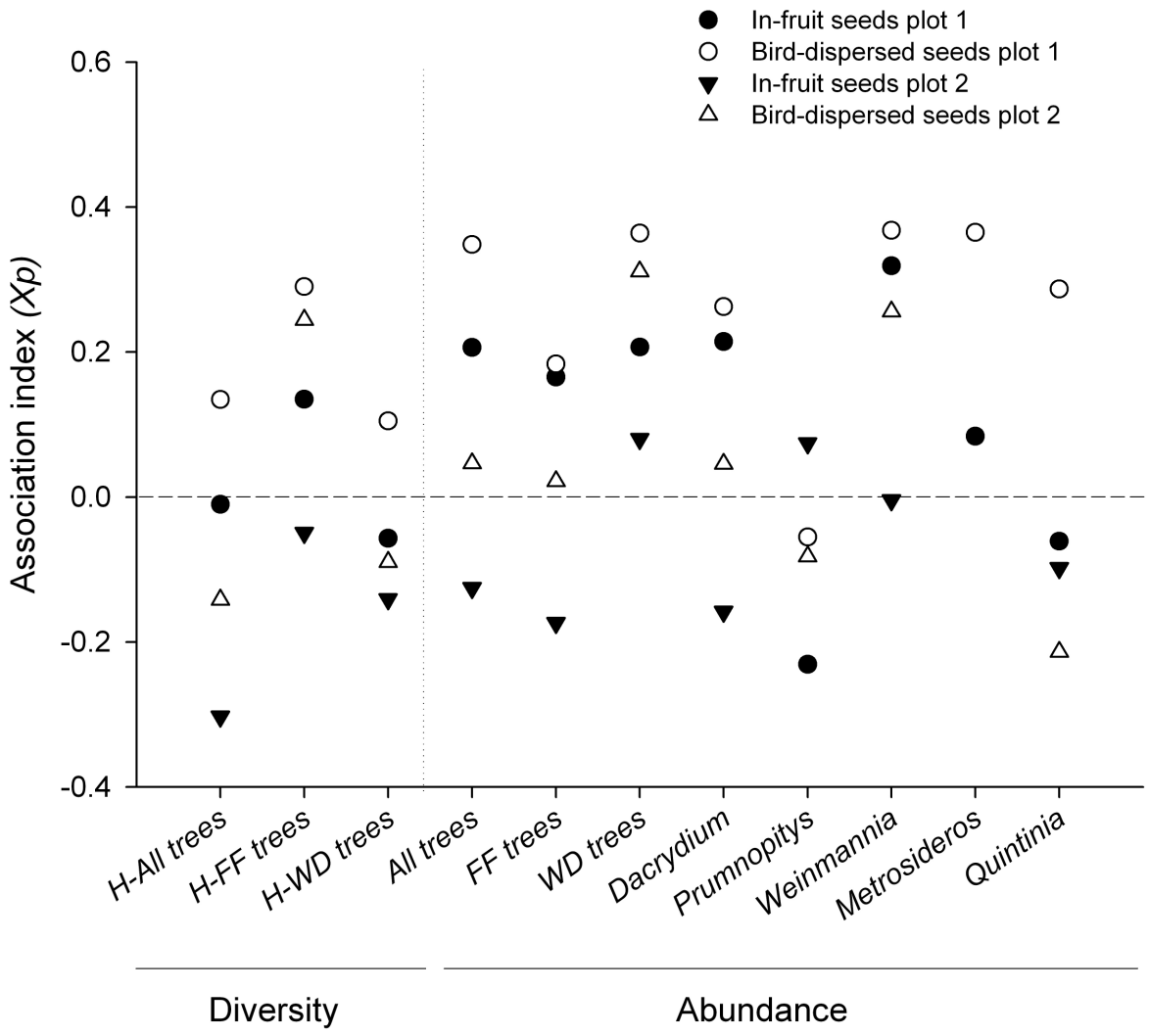


Figure 2. Association indices (*Xp*) between seed-rain (above) and basal area of trees mapped in the plots (x axis). Seed diversity includes seeds from fleshy fruited trees, shrubs and ground cover species. Diversity indices were calculated from basal areas using the inverted Simpson's index. Basal areas represent: All trees (all tree species mapped), FF trees (all fleshy-fruited trees), WD trees (all wind-dispersed trees), *Dacrydium* (basal area of *D. cupressinum*), *Prumnopitys* (basal area of *P. ferruginea*), *Weinmannia* (basal area of *W. racemosa*), *Metrosideros* (basal area of *M. umbellata*) and *Quintinia* (basal area of *Q. acutifolia*). The values of *Xp* for the association between *D. cupressinum* seed rain and trees in the plot were consistently higher for bird-dispersed seeds than for in-fruit seeds (ANOVA for condition effects $F_{1,21} = 9.22$, $P < 0.01$).

Table 3: Values of the index of association (X_p) provided by SADIE for different parameters representing the abundance and diversity of different seed types (bird-dispersed vs in-fruit seeds) and basal areas of canopy-trees. Indices indicating a significant (i.e. non-random) spatial association are in bold ($P < 0.025$).

		Seed diversity				*Dacrydium cupressinum* seeds			
		Plot 1		Plot 2		Plot 1		Plot 2	
		In-fruit	Bird-dispersed	In-fruit	Bird-dispersed	In-fruit	Bird-dispersed	In-fruit	Bird-dispersed
Basal area diversity	All	-0.010	0.135	-0.303	-0.142				
	Fleshy fruited	0.135	0.290	-0.050	0.244				
	Wind dispersed	-0.057	0.105	-0.141	-0.090				
Basal area abundance.	All					0.207	**0.348***	-0.126	0.046
	Fleshy fruited					0.166	0.183	-0.174	0.022
	Wind dispersed					0.207	**0.364***	0.080	0.311.
	D. cupressinum					0.215	0.263	-0.158	0.046
	P. ferruginea					-0.231	-0.055	0.074	-0.082
	W. racemosa					**0.319***	**0.368***	-0.005	0.256
	M. umbellata					0.084	0.365.	absent	absent
	Q. acutifolia					-0.061	0.287	-0.098	-0.214

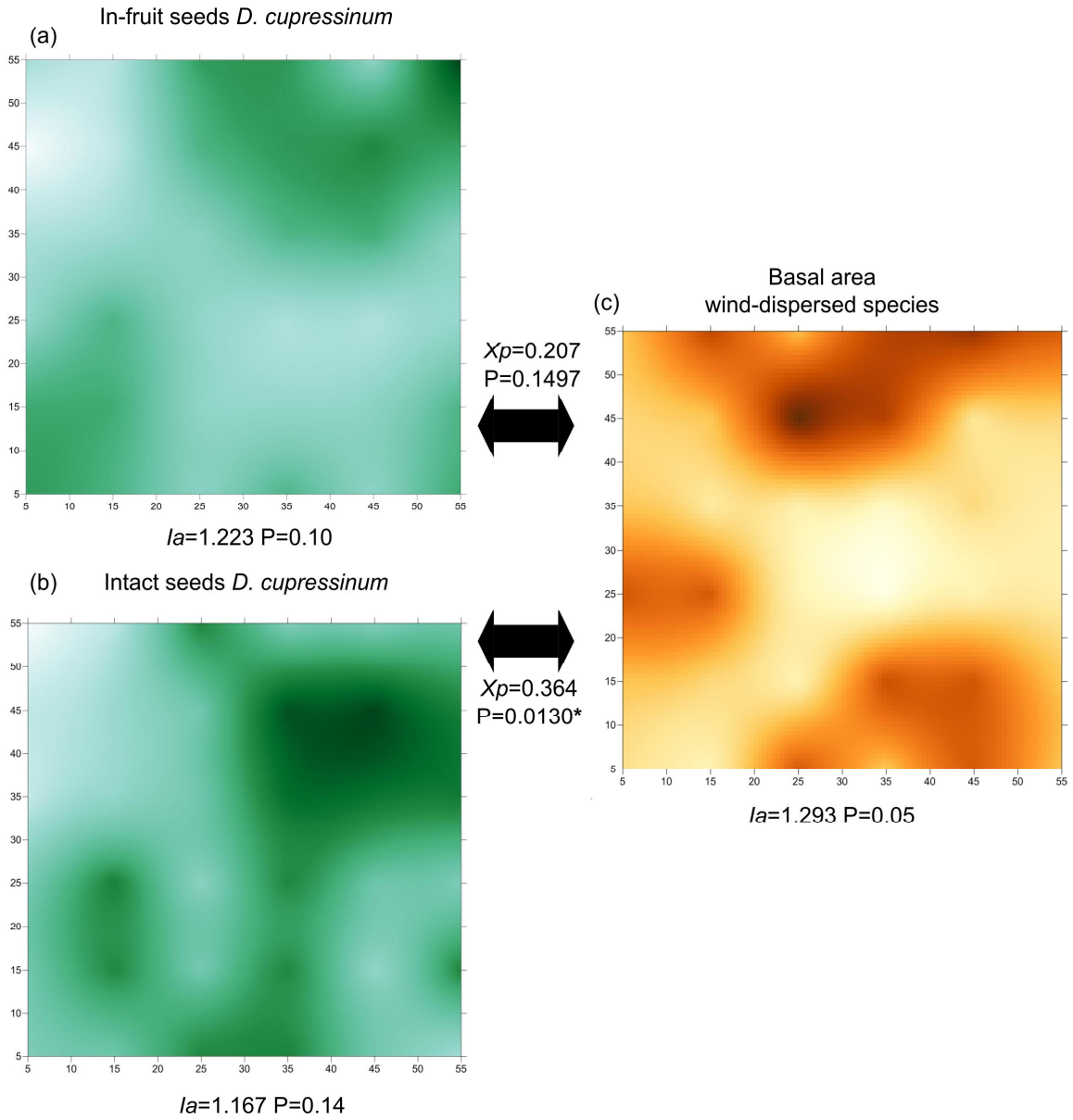


Figure 3. Image maps representing spatial pattern of seed deposition for *D. cupressinum* in-fruit seed rain (a) and bird-dispersed seeds seed rain (b), and its association with the basal area of wind-dispersed trees (c) in one of the study plots. Aggregation index *Ia* and significance level P for each dataset indicated below. Note that association index *Xp* between clusters in (a) and (c) is not statistically significant, and between (b) and (c) *is* statistically significant, represented by *. Images were constructed in Surfer software (v. 9).

The seed rain of *D. cupressinum* was not significantly associated with the basal area of conspecifics in either plot (Table 3), not for in-fruit seeds or for bird-dispersed seeds. The association was higher for bird-dispersed *D. cupressinum* seeds compared to in-fruit seeds in plot 2 but almost equal in plot 1. Overall, the association between the seed rain of *D. cupressinum* and different tree species and groups in the plots was consistently higher for bird-dispersed seeds than for in-fruit seeds (mean $Xp_{\text{non-dispersed}} = 0.34$, mean $Xp_{\text{dispersed}} = 0.20$, ANOVA for condition effects $F_{1,21} = 9.22$, $P<0.01$). The spatial association of *D. cupressinum* seeds and hetero-specific trees was not statistically significant for most of the comparisons, except for the association with *W. racemosa* trees in plot 1 (Table 3), which was significant for in-fruit and for bird-dispersed seeds. In plot 1 the negative non-significant association between in-fruit *D. cupressinum* seeds and *P. ferruginea* trees was reduced for bird-dispersed seeds. Bird-dispersed seeds of *D. cupressinum* were more associated to *M. umbellata* and *Q. acutifolia* than in-fruit seeds were, also in plot 1 (marginally statistically significant; Table 3, Fig. 2). In plot 2 the association of bird-dispersed seeds with *W. racemosa* was also higher than with in-fruit seeds, but lower with *P. ferruginea* and *Q. acutifolia* trees.

To rule out the possibility of spatial associations between adult trees of *D. cupressinum* and *W. racemosa*, the spatial association between the basal areas of the trees of both species was tested. These associations were not statistically significant in either plot (plot 1 $X_p = 0.0393$, $P = 0.409$; plot 2 $X_p = 0.1704$, $P = 0.175$).

2.5 Discussion

Seed dispersal increased seed diversity as expected. This was reflected in the increase of the values of diversity before (in-fruit) and after (all seeds) dispersal. However, the results of the spatial analysis show that this diversity is not significantly associated with any of the structures (all trees, fleshy-fruited trees or wind-dispersed trees) evaluated here, before nor after seed dispersal. I found a low but constant increase in the association between seed diversity and tree diversity, across the different dominant tree species evaluated (Table 3, Fig. 2). I was unable to find previous literature on testing this hypothesis, however, the discussion around seed dispersal and plant diversity (not seed diversity) is the spine of the theoretical framework of Janzen and Connell's hypothesis. Cadotte (2006) tested the effects of dispersal (in its broader definition) on diversity; he found that in most of the studies dispersal is related to an increase in local diversity (alpha diversity). However, this had the indirect consequence of reducing beta diversity through homogenization of the communities, finally maintaining or reducing landscape

(gamma) diversity. His study warns us about the multiple scales of the dispersal effects, and the caution I need in the interpretation of particular results in particular systems.

I evaluated the existence of spatially positive feedback (SPF) using the data for the dominant species, *D. cupressinum*. If seed dispersal is reducing SPF, then the bird-dispersed *D. cupressinum* seeds should be less associated to the canopy of *D. cupressinum* trees than in-fruit seeds, therefore the spatial association between *D. cupressinum* seeds and *D. cupressinum* trees should be reduced. If seed dispersal is maintaining SPF, then the association index should not change. In my study, I found that the spatial association between *D. cupressinum* seeds and trees is actually maintained through seed dispersal. This, however, might be an artifact of the underestimation of the situation with no dispersers with the use of whole fruits as proxy, as the numbers of in-fruit seeds in the real no-dispersal situation would be larger than the ones I estimated, and therefore, the spatial association between these two would be stronger in the pre-dispersal situation.

I found evidence for the occurrence of HST in *D. cupressinum* as seed dispersal increased the association of *D. cupressinum* seeds with heterospecific wind-dispersed angiosperm trees. These results were not constant across the two plots or across different tree species. Some trees seem to be more attractive in one plot and others in the other. *M. umbellata* and *Q. acutifolia* attracted *D. cupressinum* seeds through seed dispersal in plot 1, meanwhile *W. racemosa* was already spatially associated with *D.cupressinum* seed fall without seed dispersal. In plot 2 *D. cupressinum* seeds were more dispersed towards *W. racemosa* trees. Simultaneously-fruiting trees are not the only other attractive structures for frugivorous birds in forests, as birds select not only feeding sources but also structural components as canopy architecture or height (Jordano and Schupp, 2000), in this case, seed dispersers were actively using wind-dispersed angiosperms, the second dominant vegetational element in the plots. In a previous research, carried out near my study sites one bird species, *H. novaeselandiiae* (New Zealand pigeon) accounted for nearly 58% of all *D. cupressinum* fruit consumption (O'Donnell and Dilks, 1994). This bird presents consistent feeding and post-feeding behaviour, using trees with thin branches to feed on, and thicker branches to rest after feeding (Bell, 1996). Its feeding behaviour has been previously studied on other podocarp species (*Dacrycarpus dacrydioides*) in New Zealand. In 80% of the observations the bird flew to a heterospecific species after feeding, and nearly 90% of the *D. dacrydioides* pigeon defecated seeds fell under angiosperm trees (Bell, 1996). Consistent with those observations, in New Zealand forests Podocarpaceae seedlings and saplings have been found to be significantly more associated to *W. racemosa* trees, than to conspecific trees (*D. cupressinum* and *P. ferruginea* in Beveridge 1973; *P. ferruginea* in Lusk & Ogden 1992; *D. cupressinum*, *Podocarpus totara*, *P. ferruginea* and *D. dacrydioides* in Norton 1991). *Metrosideros* and *Quintinia* species were either absent or non-dominant

elements in the sites where these studies were carried out. Another plausible explanation is the use of *W. racemosa* and *M. umbellifera* by *T. vulpecula* (brushtail possum) as preferred food sources for flowers and leaves (Nugent et al., 2001), and seed dispersal of *D. cupressinum* seeds under the canopy of these trees during feeding episodes. However, as I did not find *T. vulpecula* faeces in the seed traps in any occasion I consider this explanation as less plausible.

2.5.1 Limitations of the study: seed types and masting

My main finding – that animal-dispersal of seeds increased small-scale seed rain diversity – was based on the comparison between bird-dispersed seed rain and the seed rain of fallen fruits, a proxy for the pre-dispersal (undispersed) seed pool. This comparison assumes the spatial patterns of undispersed fruits still conserve the imprint of initial fruiting canopies, which is only the case when not all fruits are removed by birds. Using the portion of bird-dispersed seeds relative to the total number of seeds collected, the overall removal rate in our study was 47%, showing that good numbers of both dispersed and undispersed fruits were collected. However, this overall rate is below 50% mainly because the abundant *D. cupressinum* seeds were only 33% dispersed. A number of other species collected (e.g. *Coprosma parviflora*) showed very high removal rates (> 90% seeds found as bird-dispersed), potentially leading to underestimation of diversity in the undispersed seed rain. However, these are mostly less-common lower-stature plants, so the failure to collect many undispersed seeds may not reflect very high removal rates by birds; rather it may reflect that their undispersed fruits are so localized that few found their way into seed traps. Therefore, the data should still fairly reflect the wider spatial patterns of diversity in both dispersed and undispersed fruits.

Dacrydium cupressinum is a mast seeding species (Norton and Kelly, 1988); however, the two fruiting seasons sampled during my study were low fruiting seasons. Mast-fruiting can be expected to have a large impact in seed deposition, with numbers of seeds so large that this could erase any particular association and homogenize the seed fall throughout the forest floor. However, Herrera et al (1994) found that seed fall of *P. latifolia*, a fleshy fruited Mediterranean tree, even during a masting event year was biased towards different microhabitat in the forest, still determined by habitat use preferences of the seed dispersers. Masting events do not necessarily always translate into increased reproductive success (Lázaro, Traveset, and Méndez, 2006). It is difficult to predict what patterns could be expected from a masting event in *D. cupressinum*, as seed disperser populations have been reduced with the introduction of exotic predators, and therefore frugivores could be satiated too soon to make a difference in seed deposition patterns relative to a normal year (Kelly and Sork, 2002). If this were the case, the increase in fruit crop would only increase the number of whole fruits dropped below the canopy of the parent canopy.

2.5.2 Possible outcomes of the increase in seed-fall diversity

This increase in diversity implies that seeds are being deposited in a more multispecific context (deposited with seeds from other species) than how they are produced, however, the effects of this on seed survival are species-specific and context dependent. In a study in a mixed podocarp-angiosperm forest of Fiordland National Park, south of my study site, Wilson et al. (2007) found that depending on tree neighborhood and forest type (alluvial forest vs terrace forest) seed predation on *D. cupressinum* and *P. ferruginea* seeds varied. In terrace forests seed predation of *D. cupressinum* was higher in *D. cupressinum* neighbourhoods (characterized in a radius of 15 m surrounding the predation stations), therefore, higher in monospecific context, and lower in *Podocarpus totara* neighbourhoods (more diverse context). On the contrary, seed predation on *Prumnopitys ferruginea* seeds followed the reverse pattern (Wilson et al., 2007). Studies in other temperate forests, northern Spain (secondary forest, García et al. 2007) and South Carolina, USA (hardwood forest, Kwit et al. 2004) also show that the effects are species-specific, and also dependent on the background frequency of the heterospecific seeds. To my knowledge, there is a lack of research on the effects of multi-specific seed rain on seed predation and seedling survival, and this is even more on temperate ecosystems.

In my research I found that bird-dispersed *D. cupressinum* seed fall is not significantly associated to con- and to heterospecific trees. There were, however, small increases in the degree of association between *D. cupressinum* seeds and some heterospecific trees (Table 3). In general, survival under conspecific plants is low, due to high seed predation or fungal attack during the seed stage, and biotic factors during seedling stage (Wilson et al., 2007; Hampe et al., 2008; Alvarez-Loayza and Terborgh, 2011). Seed mortality due to seed predation can be also influenced by heterospecific seed densities under heterospecific canopies, and the output of this interaction is however species-dependent, depending on the preferences of seed predators on the different seeds offered (Kwit et al., 2004; García et al., 2007; Wilson et al., 2007). Even though I do not have information regarding seedling recruitment in my site, previous research have shown that seed deposition numbers can outnumber seed mortality due to predation, with sapling densities matching seed fall distribution particularly away from con-specific canopies (Russo and Augspurger, 2004; Lázaro, Traveset, and Castillo, 2006). Per capita success of dispersed seeds can indeed be many times higher than that of un-dispersed seeds (Terborgh et al., 2011), increasing its importance at individual (seed) level over fruit crop level.

2.5.3 Concluding remarks

The importance of seed dispersal by birds for determining the spatial patterns of plant recruitment in temperate forests is still an open question. My study is the first to demonstrate the increase the seed diversity at ground level, and to evaluate the relative importance of heterospecific seed transfer and

spatially positive feedback on this result. Seed dispersers are changing seed deposition patterns, setting new "starters" for community succession. This is only one of three possible effects of HST on the community, the other two being an increase in the diversity of microsites (physical microsites) reached by the seeds, and an increase in the diversity at microsites, i.e. new seed combinations in the destination microsite. This is not an uncommon phenomenon in temperate forests (Jordano and Schupp, 2000; Kwit et al., 2004; García et al., 2007), however the fate of the seeds in these variety of situations should be explored more deeply and compared to the absence of dispersal situation. The diversity of microhabitats reached through bird-mediated seed dispersal should improve the chances for successful recruitment of all the dispersed species. Through changes in the selective pressure exerted by density- and frequency-dependent processes, the effects are expected to be species-specific (Kwit et al., 2004; García et al., 2007), ultimately affecting the community structure and composition.

CHAPTER 3

Pelorus River, photo taken from Pelorus Brige

3 Biotic seed dispersal decreases seed rain heterogeneity in a mixed temperate forest

3.1 Abstract

1. Seed dispersal can increase local species diversity by moving propagules away from conspecifics, creating new combinations of seeds on the ground. Hence, it is possible that frugivore activity changes ground-level homogeneity of seeds at a propagule scale, therefore decreasing the heterogeneity in species composition. To my knowledge, this change and the mechanisms for it have not yet being investigated.
2. Using a 12-year dataset on seed fall I analyzed the changes in ground-level heterogeneity generated by bird-dispersed seed rain (propagule-scale) relative to the canopy composition (adult-scale). I did this on six species with different fruit sizes and dispersal assemblages, co-occurring in a temperate forest in New Zealand. I compared the canopy composition above each seed trap to the seed rain of bird-dispersed seeds inside of the seed traps. I also identified the tree species that attracted seeds from heterospecific canopies (seed importers) and tree species whose seeds were more likely to be found under heterospecific canopies (seed exporters).
3. A Non Metric Multidimensional Scaling analysis demonstrated that the differences in species composition between sampling points (seed traps) was larger for tree canopies than for dispersed seeds. The mechanism for this change was explained through different tree species acting as seed importers and/or exporters, although these patterns were not explained by fruit size or the richness of the disperser assemblages.
5. The dispersers reduced the heterogeneity of the seed rain through the process of seed transfer between heterospecific canopies. This process is determined in different intensities by the characteristics of the plants studied and the dispersal assemblages. The existence of positive interactions between heterospecific seeds and canopies allow for seed presence away from conspecific canopies and can increase plant recruitment probability. Post-seed dispersal environmental filters will modify the template set by the seed rain, adding heterogeneity into the communities.

3.2 Introduction

The movement of individuals between communities (in the case of seed dispersal, seeds between trees) can increase local diversity with either new individuals arriving from external communities, or individuals

moving inside the local community. In a meta-analysis of 23 studies, representing 50 experiments, Cadotte (2006) found that dispersal significantly increased diversity at the local scale (alpha diversity), but reduced it at a medium scale (beta diversity) homogenizing of the communities, having a final effect of maintaining or reducing gamma-diversity (landscape scale). Homogeneity in tree composition implies similarity between the components of the community. Homogeneity and heterogeneity in the species composition in a plant community occur at different stages of the plant life history: recruitment stage (propagule or seed), seedlings, saplings, and adult stage (trees and canopies), and it can be defined at different scales within a community, affecting the way a community is structured and how diversity persists over time.

Spatial heterogeneity in seed rain composition is the result of the process of seed transfer between con- and hetero-specific canopies. Canopy composition is the most influential factor for seed rain composition. In the case of animal-dispersed plant species the type of dispersal agent will influence seed removal rates and seed deposition patterns. Fruit crop also strongly determines removal rates, with larger crops attracting more dispersers and therefore, larger numbers of seeds removed from the canopy (Sallabanks, 1993; Takahashi and Kamitani, 2004; Saracco et al., 2005; Herrera et al., 2011). Fruiting neighborhood is also influential on fruit removal rates (Sallabanks, 1993; Carlo, 2005; Saracco et al., 2005; Carlo and Morales, 2008; Blendinger and Villegas, 2010). However, its effects are subject to the identity of the accompanying plant species, for example, conspecific neighbors can compete with the target tree, reducing the fruit removal by frugivores, but heterospecific neighbors can increase removal rates by attracting a more diverse assemblage of dispersers (Takahashi and Kamitani, 2004). Something similar has been found when the focus is on seed movement; the principal factor that determines the arrival of conspecific seeds below a plant with fruits is its fruit crop size. However the arrival of heterospecific seeds is determined by the neighborhood and the habitat characteristics (Blendinger et al., 2011). Some of the factors influencing seed dispersal patterns may be correlated; for example species with small fruit size are often the ones with largest fruit crops , and with the largest array of seed dispersers (Howe et al., 1982; Greene et al., 1999). In the case of systems where the largest seed dispersers have been reduced in richness or populations, the relationship between trees species and their dispersers will become stronger, increasing the difference in the dispersal assemblages between large and small-fruited species, or replacing the original large dispersers with exotic species. All these factors will affect the structure of the spatial deposition of the seeds at ground level, to what extent new combinations of seeds are generated, and how this process of seed dispersal (involving all the determinants) will increase or decrease the heterogeneity in species composition.

But, are all trees species equally contributing to the process of seed dispersal between canopies, and the shift in the heterogeneity in seed rain species composition? Implicit in the process of seed removal by frugivores, is the fact that most of the times a bird is feeding on a tree, at the same time it will defecate seeds previously consumed, either from a con- or an hetero-specific tree (García et al., 2007). Trees with high seed removal rates would behave as "seed exporters" inside of the community, but this will only impact species composition in the community if the seeds are exported towards heterospecific canopies. In the case of trees with high fruit removal rates but seed dispersers feeding solely on conspecific canopies the output will be just a spatially positive feedback (SPF, Chapter 2) on the seed rain under its canopy. But it is likely for these trees to have also high rates of arrival from hetero- and con-specific seeds, brought by the dispersers. Trees with frequent arrival of heterospecific seeds are known as "dispersal foci" in the seed dispersal literature. These trees usually receive heterospecific seeds under their canopies, from other tree species with who they share the same disperser assemblage (Herrera et al., 1994; Clark et al., 2004; Kwit et al., 2004). Here, I will call these trees "seed importers", as they "import" seeds from heterospecific canopies within the community, increasing diversity in the seed rain falling under their canopy. The functional roles of trees as seed exporters/importers in the community will affect the species composition in the seed rain stage, and "sow" the potential for future changes in species composition at a small scale (tens of meters) in the community. If more tree species act as seed importers and seed exporters, increasing heterospecific seed transfer (HST, Chapter 2) I would then expect a decrease in the heterogeneity of species composition in the seed rain, compared to the heterogeneity of species composition in the canopy of the community.

My aim is to analyze the heterogeneity of species composition in the seed fall of animal-dispersed plant tree species, to identify the mechanisms driving the observed patterns. To do this I use a 12-year dataset on the seed fall of six fleshy fruited tree species with different fruit sizes (range 2.5 - 15.5 mm diameter) in a temperate forest in New Zealand: *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Prumnopitys taxifolia*, *Elaeocarpus dentatus*, *Prumnopitys ferruginea* and *Beilschmiedia tawa*. I expect a decrease in the heterogeneity of species composition in the seed rain as a consequence of bird-mediated seed dispersal, and differences in the functional roles of the trees as exporters and importers of seeds, as the mechanism for the observed patterns. Specifically, I expect that: (1) Species composition in the seed rain will be more homogeneous than canopy composition at a local (tens of meters) scale (2) The species with smaller fruits and more diverse disperser assemblages will function as seed exporters and importers in the community (3) Species with larger fruits will concentrate more conspecific seeds, as well as seeds from the other large fruited trees, as fewer and more specialized dispersers will forage in their canopies.

3.3 Methods

3.3.1 Study site and species

I used a 12-year dataset on seed fall in a lowland temperate forest at Pelorus Bridge Scenic Reserve (41°18'S - 173°35'E) in the Marlborough district, New Zealand (Clout et al., 1991, 1995). I used an old-growth (never logged) 100-ha terrace in the Reserve with a relatively diverse canopy. The area has a moist oceanic climate. The annual rainfall in Nelson, 24.3 km west of Pelorus is 800 mm/year, the summer (January) average minimum temperature is 9.2°C, and maximum 27°C ,and in winter (July) -1.3°C min and 16.1°C max (New Zealand Meteorological Service, 2012). I focused on six of the most common fleshy-fruited tree species: *Beilschmiedia tawa* (Lauraceae), *Prumnopitys taxifolia, Dacrycarpus dacrydioides*, *Prumnopitys ferruginea*, *Dacrydium cupressinum* (all Podocarpaceae) and *Elaeocarpus dentatus* (Elaeocarpaceae) (Table 1). Wind-dispersed trees *Weinmannia racemosa* (Cunoniaceae) and *Nothofagus solandri* (Nothofagaceae) are also well represented in the remnant (Clout et al., 1991, 1995). The fruiting phenologies of my six study species overlap in the study site with 78-95% of all seeds caught between January and May, at least 95% of all seeds fell by August (Fig. 1). The four podocarp species (Table 1) bear seeds enclosed by or attached to fleshy tissue. Two of them (*D. cupressinum* and *D. dacrydioides*) present seeds attached to an aril, and the other two (*P. ferruginea* and *P. taxifolia*) a seed enclosed by fleshy tissue. These structures constitute functional fruits in terms of their attractiveness to frugivores (Beveridge, 1964), I therefore will call them "fruits" throughout this study. The six species selected embrace a range of medium to large fruit sizes in the New Zealand flora (Kelly et al., 2010; Lord, Markey, & Marshall, 2002), from *D. cupressinum* at 2.5 - 6.0 mm long to *B. tawa* up to 15.5 mm diameter (Table 1). All species carry single-seeded fruits. The different fruit sizes determine disperser assemblages partially distinct from each other (Table 1), with the smallest fruits having a wider range of dispersers when compared to larger-fruited trees (Lord et al., 2002; Kelly et al., 2010). In particular, *Anthornis melanura* (common bellbird) and *Zosterops lateralis* (silvereye) mainly eat fruits smaller than 7-9 mm width (Kelly et al., 2010).

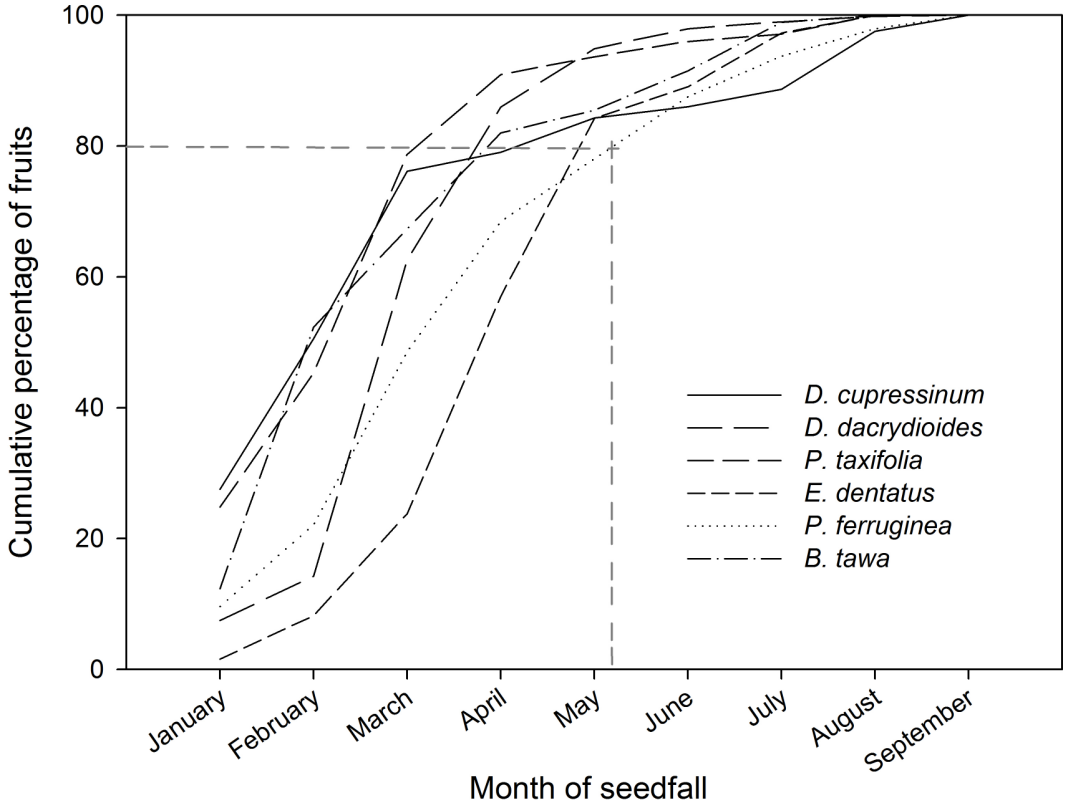


Figure 1. Fruiting phenologies for the studied species based on 5 years of data. Only years with monthly collections were used (1986-1989 and 2010) Month represents the production date (collections were always carried out on the first day of the next month). Grey dotted lines indicate the time in the year when at least 80% of all seeds have fallen (near May).

3.3.2 **Seed rain**

To estimate a robust interspecific seed fall pattern across many years with overcoming intermittent crops (Norton and Kelly, 1988), in 1986 one seed trap was placed under the canopy of 5-10 reproductive adults (females in dioecious species, Table 1), belonging to the six different species. Five seed traps were placed under *D. cupressinum* trees (due to restricted availability of female adults) and 10 under each of the other species (total n=55). Seed rain was monitored between 1986-1990, and 2004 to 2010. As four trees could not be relocated in 2004, four new trees were added to replace the missing (number of seed traps n=51

1986-1990, n=55 2004 and 2010). The seed traps used in 1986-2009 were 0.10 m^2 (0.37 m diameter) cones suspended 1 m above ground (Appendix 1). In 2010 seed traps were replaced by larger ones, with a sampling area of 0.28 m^2 and height of 1.20 m above ground (Appendix 1). Seed rain was collected from 1st January each year, and then on the first day of every month or every second month, between February and October (fruiting season). Samples from seed traps were air-dried and seeds belonging to the six species of interest were identified. During 1986-1990 seeds were classified as: bird-dispersed (clean seeds, with neither pulp or aril attached), damaged seeds (insects or mammals) and whole fruits under conspecific nominated canopies. Seeds not falling in these categories were not recorded (e.g. whole undispersed fruits from tree species different from nominated canopy above seed trap). Between 2004 and 2010 non-viable fruits (aborted, green fruits, which are not considered further in this chapter) and all whole undispersed fruits (ripe and overripe fruits) were also recorded. As my interest was bird-mediated seed dispersal, I grouped the data as follows: "total seeds" (whole fruits + bird-dispersed seeds + insect damaged seeds + mammal damaged seeds) and "bird-dispersed seeds" (hereafter "dispersed seeds"). There are no native mammalian dispersers at my site.

To analyze the influence of the canopy composition above the seed trap on the seed rain I characterized the seed traps in the field recording the following: species identity of canopy above seed trap, trunk diameter at breast height (dbh) and distance from the centre of the seed trap for each corresponding tree (canopy owner, maximum distance measured 7 m). Reproductive canopies were identified (as four of the studied species are dioecious, Table 1) using the information on whole fruits collected between years 2004-2010 and the presence of canopy above seed traps. Thus, each seed trap was determined to catch from between a minimum of one and a maximum of three overhead species. The final numbers of seed traps per target species are presented in Table 1. All analyses were done using the reproductive canopies above seed traps, instead of all canopies.

I also analyzed the nutritional contents and secondary compounds of the fleshy tissue in the fruits of five of the six species studied, and its correlation with the percentage of fruit crop collected as bird-dispersed seeds.

Table 1: Characteristics of the species studied. H = plant height, FD = fruit diameter, SD = seed diameter (means). N = number of seed traps underneath. Traps column represent the percentage of all seed traps that received dispersed seeds of each particular species. Seeds column represent the number of dispersed seeds collected during the study. Total number of seed traps was n=51 for the period 1986-1990 and n=55 for 2004-2010. Seeds per seed trap represent the median number of seeds across all seed traps (year pooled). Numbers between brackets in median column indicate the minimum and maximum number of seeds collected in one seed trap across all years across all seed traps. Dispersers are arranged from the species with the smallest gape size (left) to largest (right) according to Kelly et al. (2010). Bird species names codes as follows: Zl = *Zopterops lateralis* (silvereye), Am = *Anthornis melanura* (bellbird), Tm = *Turdus merula* (blackbird), Pn = *Prosthemadera novaeseelandiae* (tui), Sv = *Sturnus vulgaris* (starling), Tp = *Turdus philomelus* (song thrush) and Hn = *Hemiphaga novaeseelandiae* (kereru). * = exotic species.

Species	Family	Plant sexuality	H (m)	FD (mm)	SD (mm)	N	Traps (%)	Seeds	Seeds per seed trap	Dispersers						
										Zl	Am	Tm*	Pn	Sv*	Tp*	Hn
D. cupressinum	Podocarpaceae	Dioecious	35	4	3.2-3.8	12	87	1017	7 (0-357)	1	1	1	1			1
D. dacrydioides	Podocarpaceae	Dioecious	50	5.11	4.37	10	100	44617	116 (2-6117)	1	1	1	1	1	1	1
P. taxifolia	Podocarpaceae	Dioecious	25	9.4	6.65	13	100	4611	30 (2-498)	1	1	1	1			1
E. dentatus	Elaeocarpaceae	Hermaphrodite	15	9.2	6.75	10	25	45	0 (0-12)							1
P. ferruginea	Podocarpaceae	Dioecious	25	13	11	10	89	883	5 (0-130)		1	1	1			1
B. tawa	Lauraceae	Hermaphrodite	24	15.5	11.4	20	82	321	2 (0-63)				1			1

Plant families and sexuality from Salmon (1980). Tree heights were obtained from Allan (1961), fruit diameters from Kelly et al. 2010, and this study. Seed sizes are from Webb & Simpson 2001, this study and Kelly et al. 2010, dispersers from Kelly et al. 2010 and O'Donnell & Dilks 1994.

3.3.3 **Data analysis**

3.3.3.1 Seed removal rates and species composition at canopy and seed rain levels

I first evaluated the relationship between total seed crop and percentage of bird-dispersed seeds per plant species. Only years 2004-2010 could be included in this analysis, as previous years had incomplete counts of whole fruits. I then represented the seed rain of each of the studied species, under the canopy of conspecific and heterospecific trees using manually constructed bipartite networks, with the information on seeds (whole plus bird-dispersed, period 2004-2010) and dbh (diameter at breast height, 1.37 m above ground surface) of the trees with canopy above these seed traps. Only a subset of the seed traps (the ones with a single canopy species above) was used for this representation (*D. cupressinum* n = 4, *D. dacrydioides* n = 7, *P. taxifolia* n = 3, *P. ferruginea* n = 8, *B. tawa* n = 6). I then calculated the proportion of basal area corresponding to each of the tree species in relation to the total basal area accumulated surrounding the 28 seed traps. I did the same with the number of seeds collected (all seeds and bird-dispersed seeds) of the different species.

To represent the influence of the canopy above the seed traps in terms of the possible contribution to the fruit crop, and include it in the analyses, I generated a "canopy index", based in a modification of the Hegyi index for tree competition (Das et al., 2008). I used the following formula to calculate the influence of each canopy species above the seed trap

$$Canopy\ index_{i\ on\ j} = \frac{(DBH_i)^2}{Dist_{ij}}$$

where DBH_i is diameter of the tree *i* with canopy above seed trap *j* and $Dist_{ij}$ is the distance between the centre of the seed trap *j* and the centre of the tree trunk *i*. Canopy indices were summed by species above each seed trap. Thus, each seed trap had a corresponding canopy index per canopy species. For New Zealand trees a variable (at inter-specific level) relationship between DBH and canopy area (m^2) have been found (Norton et al., 2005). However, as my interest is on fruit crop size I am more concerned with biomass (wich is expected to be closely related to DBH) than with canopy area as discussed in Norton et al. 2005.

To examine the significance of the differences between species composition in the canopy above the seed traps and in dispersed-seeds collected in the seed traps (all years) I used a permutational multivariate analysis of variance (MANOVA). This analysis implements a multivariate analysis of variances using distance matrices (Oksanen, 2011), and it is able to detect differences in the location (centroid or mean of sampled points) or dispersion (variance or cloud/hull) of two groups in the multivariate space (Anderson, 2001). Therefore, a significant P-value in PERMANOVA may be

indicative of differences in either of these parameters and the results of this analysis should be interpreted carefully. Function "adonis" (in vegan v.2.0-2 package, Oksanen et al. 2011) in R statistical software (R Development Core Team, 2011) partitions dissimilarities for the sources of variation (seeds and canopies) using Bray-Curtis (Sørensen) distances, and 1 000 permutation tests to inspect the significance of those partitions. Then, to visualize the multivariate patterns of seed rain and canopy composition in a multidimensional space I used non-metric multidimensional scaling (NMS). NMS has been described as the most robust unconstrained ordination method in community ecology (McCune and Grace, 2002). I used Bray-Curtis distance measures calculated by the "metaMDS" function in vegan package (v.2.0-2). NMS can, however, converge on unstable locally optimal solutions that are not robust. To avoid this possibility I used 1 000 random starts to find the best global solution. I ran consecutive iterations until convergent solutions with the minimum stress were found. The stress represents the goodness of fit of the ordination, based on the differences between the distance measures in the data and the distances in the ordination (McCune and Grace, 2002). The principal components of the NMS are then rotated so that the largest variance between the sites (seed traps) scores are on the first axis (Oksanen, 2011). To avoid undesired effects due to differences between the scale of the variables estimated (canopy index for canopy composition, and seed counts for seed rain) both variables were transformed to proportions, with the sum of all canopy indices above each seed trap adding up to 1, and the sum of all seeds collected inside each seed trap adding up to 1. Recently, the use of Bray-Curtis distances have been criticized as it is sensitive to differences in variance between the groups evaluated, something that could not be fixed with transformation or standardizations (Warton et al., 2012). However, due to time constraints, amendments of this analysis will be carried out for a manuscript to be published in the future.

3.3.3.2 Effects of tree canopies on seed rain

To disentangle species-specific canopy effects on the seed rain of each one of the target species I ran generalized linear mixed effects models (GLMMs). Ecological data, such as seed rain data, are frequently non-normal, over-dispersed and/or present an excessive number of zeros, however GLMMs can deal with these (Bolker et al., 2009; Zuur et al., 2009). After visual inspection of the response variable (bird-dispersed seed rain per species, all years) I ran the models using negative binomial response distributions. Package glmmADMB in R software (version 0.7 , Skaug et al. 2011) supports negative binomial distributions, can handle zero-inflated data (ZI) and allows incorporation of random effects in the models. This package offers two optional parameterizations for the negative binomial distribution: the standard negative binomial (NB) distribution parameterization $variance = \mu(1 + \mu/\propto)$ and an alternative parameterization (NB1) $variance = \propto \mu$ (for details see package supporting material, Skaug et al. 2011).

I used the Akaike Information Criterion corrected for small sample sizes (AICc) to select the distribution that best fit the data, by comparing the full models run with different (NB, ZINB, NB1 and ZINB1) response distributions (Zeileis et al., 2008; Skaug et al., 2011). AICc is based in the magnitude of difference between models, in terms of their potential predictive power (Bolker et al., 2009). In this procedure, the model with the smallest value of AICc is estimated to be the closest to full reality, therefore, the best model of the set (Anderson, 2008). The full model included the canopy indexes of the six species as fixed predictor variables, with no interaction terms. Because observations from seed traps among years are not independent I specified seed trap as a random effects factor. My response variable was the number of dispersed seeds of each species (six species = six independent full models). Once the best response distribution (NB, ZINB, NB1 or ZINB1) was found, I started a second model selection procedure using an information-theoretic approach (Burnham and Anderson, 2002). In this approach a set of plausible models (set of alternative hypotheses) are tested and ranked using AICc. Multimodel inference provides the possibility of giving different weights (strength of evidence) for different alternative hypotheses (Burnham et al., 2011). As previous knowledge of the system under study was not enough to make sensible predictions I had no a priori basis for predicting the effects of each heterospecific canopy on the seed rain of each of the six species; I therefore tested all possible models (all-subset candidate set approach) using the "dredge" function in MuMIn package (Barton, 2012). This approach has previously been described as "poor science" (Burnham and Anderson, 2002), however, constructing prior hypotheses on the base of poor knowledge of the system would take us to a biased selection of the best model (as only models entered are considered in the analysis). My approach allowed us to evaluate the specific effect of each of the canopy species alone or accompanied by other species on the seed rain of each given species. For each model in the set of models I calculated AICc, ΔAICc, $L(g_i|x)$, w_i and the evidence ratio. ΔAICc is the difference between the model with the lowest AICc in the set and the model under scrutiny; therefore, ΔAICc is used to rank the models. $L(g_i|x)$ is calculated as the likelihood of a model g_i given the data x, it represents the relative strength of evidence for each model in the set. w_i is the Akaike weight of the model, it represents the probability of each model in the set being the best model ($\sum w_{i\ model\ set} = 1$). Finally, evidence ratios (ER) are relative to the other models in the set, and give a quantification of the weight of the evidence for each of the models in the set in a more intuitive manner (Burnham and Anderson, 2002). I estimated the relative importance of the predictor variables for each species adding up the Akaike weights (w_i) for each model in which that variable appears (Burnham and Anderson, 2002; Symonds and Moussalli, 2011). As the information relevant for my question would be present in all of the models tested, and to overcome model uncertainty in the cases where the best AIC model is not strongly weighted ($w_i \leq 0.9$, all cases in this study), I used a "full model averaging"

approach. In full model averaging the estimate of the parameter of interest is weighted by the model probability (w_i) in each model (when parameter is absent from model it estimate is replaced by zero), and summed across all models giving a "model averaged estimate" for each parameter of interest (Burnham and Anderson, 2002; Symonds and Moussalli, 2011). I also calculated the unconditional standard errors (Burnham and Anderson, 2002) for the model averaged estimates using the function "model.avg" in MuMIn package (Barton, 2012). Approximate 95% confidence intervals for the averaged parameter estimates were calculated using two times the standard error estimates. The use of model averaging reduce the bias of the estimators, and it can increase precision, compared to the use of the estimators of the "best model" (Burnham and Anderson, 2002). This method is not appropriate when non-linear models are used; this is, however, not my case. All statistical analyses were carried out with R 2.14.1 (R Development Core Team, 2011).

3.4 Results

3.4.1 Seed removal rates

During the 12 years sampled, a total of 77 823 seeds were counted and identified (total seeds). Between years 1986 and 1990 whole fruits were only counted when found under the canopy of a conspecific nominated canopy, therefore, the percentage of bird-dispersed seeds from the total is overestimated for this period. Total number of seeds collected to 1990 was 29 140, and 20 921 (72%) of them were bird-dispersed seeds. From 2004 onwards all fruits from the six species studied were counted and identified. Total numbers from 2004 on was 48 683 total seeds, of this, 26 055 were bird-dispersed seeds (54%). The percentage of seed traps that captured seeds of each of the six species at any time during the whole study varied from 100% (*D. dacrydioides* and *P. taxifolia*) to 25% (*E. dentatus,* Table 1).

The estimated number of seeds per square meter collected was also variable between species and between years (Table 2). Total seed rain numbers were dominated by *D. dacrydioides* (mean seeds/m^2 = 695.8), being 45 times larger than the seed rain of the lightest fruit producer (*E. dentatus* = 15.3 seeds/m^2). The two angiosperms (*E. dentatus* and *B. tawa*) had fruit crops of the range of 15 to 21 seeds m^{-2}. The coefficient of variation for the different species across years was also lower for large-fruited trees, but variable for medium and small-fruited trees (*D. cupressinum*, *D. dacrydioides*, *P. taxifolia* and *E. dentatus*). Although *D. dacrydioides* had the largest fruit crop, it was not the most variable species between years. In general, all species produced at least some fruit each year, except for *D. cupressinum*, which had three of the 12 years with no seed rain recorded (1988 total seed rain may be underestimated). Total seed rain of *D. cupressinum* was consistently low, except for 2005, which was anticipated and

followed by years with no seeds. The proportion of the fruit crop that was collected as dispersed-seeds was higher for small-fruited species (the ones with the most diverse assemblage of seed dispersers, *D. cupressinum* and *D. dacrydioides*, mean 82.7% and 76% respectively), low for mid-fruited species (*P. taxifolia* and *E. dentatus*) and medium for large-fruited trees (*P. ferruginea* and *B. tawa*). *Prumnopitys taxifolia* and *P. ferruginea*, both species with similar dispersers assemblages (Table 1), presented different percentages of dispersed-seeds (*P. taxifolia* mean = 11.6%, *P. ferruginea* = 47.4%). For *D. cupressinum* and *D. dacrydioides* the variability of the proportion of the total fruit crop dispersed was smaller than the total fruit crop variability, and it was more variable for *E. dentatus* (Table 2). *Beilschmiedia tawa* was the only species where total seed crop was significantly correlated to the percentage of bird-dispersed seeds across the years ($n= 7$ $\rho = -0.82$, $P < 0.05$; Appendix 2).

The percentage of dispersed fruit crop was significantly correlated with tree height ($P < 0.05$, Fig 2), and weakly correlated with percentage of fleshy tissue ($P = 0.06$, Fig. 2). For full results on nutritional contents and correlations with bird dispersed fruit crop see Appendix 3.

Table 2: Summary of the seed rain across years for *Dacrydium cupressinum* (Dc), *Dacrycarpus dacrydioides* (Dd), *Prumnopitys taxifolia* (Pt), *Podocarpus ferruginea* (Pf) and *Beilschmiedia tawa* (Bt). Species are ordered from left to right by increase in fruit size. The number of total seeds collected between 1986 and 1990 are sub-represented, as only the whole fruits collected under the canopy of conspecific nominated trees were counted. Zero values of seed rain per square meter in Dc represent real zeros. SD = standard deviation, CV = coefficient of variation.

	Seeds m^{-2}						*Percentage of dispersed seeds*					
Year	*Dc*	*Dd*	*Pt*	*Ed*	*Pf*	*Bt*	*Dc*	*Dd*	*Pt*	*Ed*	*Pf*	*Bt*
1986	12.4	3219.5	8.0	142.9	32.7	68.0	64.7	86.7	31.8	1.7	48.3	0.5
1987	2.4	76.0	407.8	0.5	10.2	0.4	7.7	12.4	61.1	0.0	87.5	50.0
1988	0	65.5	206.7	24.2	18.9	44.4	NA	80.8	41.1	6.8	52.9	2.5
1989	2.7	302.2	6.0	1.1	16.0	0.5	100.0	86.6	66.7	50.0	69.3	33.3
1990	0.2	1198.0	363.6	50.9	15.3	16.2	100.0	80.1	35.8	5.7	77.4	6.7
2004	0	1457.5	240.5	12.2	34.2	46.0	NA	71.9	0.7	0.0	27.7	9.9
2005	107.3	458.5	44.0	59.5	20.9	11.3	96.9	96.6	6.2	0.0	58.3	38.7
2006	0	210.9	4.0	0.4	5.3	6.2	NA	95.2	31.8	0.0	75.9	35.3
2007	12.4	587.5	203.3	23.3	20.2	8.5	100.0	46.1	2.2	0.0	50.5	74.5
2008	14.4	446.9	22.9	7.6	23.6	38.5	100.0	87.5	0.0	0.0	31.5	11.3
2009	19.3	1297.8	4.0	3.5	44.7	0.9	100.0	89.9	18.2	0.0	47.6	40.0
2010	52.1	411.6	571.2	0.8	33.8	35.8	16.3	44.9	22.3	30.8	40.5	33.2
Mean*	29.3	695.8	155.7	15.3	26.1	21.0	82.7	76.0	11.6	4.4	47.4	34.7
SD*	38.6	481.0	207.5	21.0	12.7	18.4	37.1	22.3	12.5	11.6	16.5	21.6
CV*	1.3	0.7	1.3	1.4	0.5	0.9	0.4	0.3	1.1	2.6	0.3	0.6

* only years 2004-2010 (only years with full information on whole fruits) considered

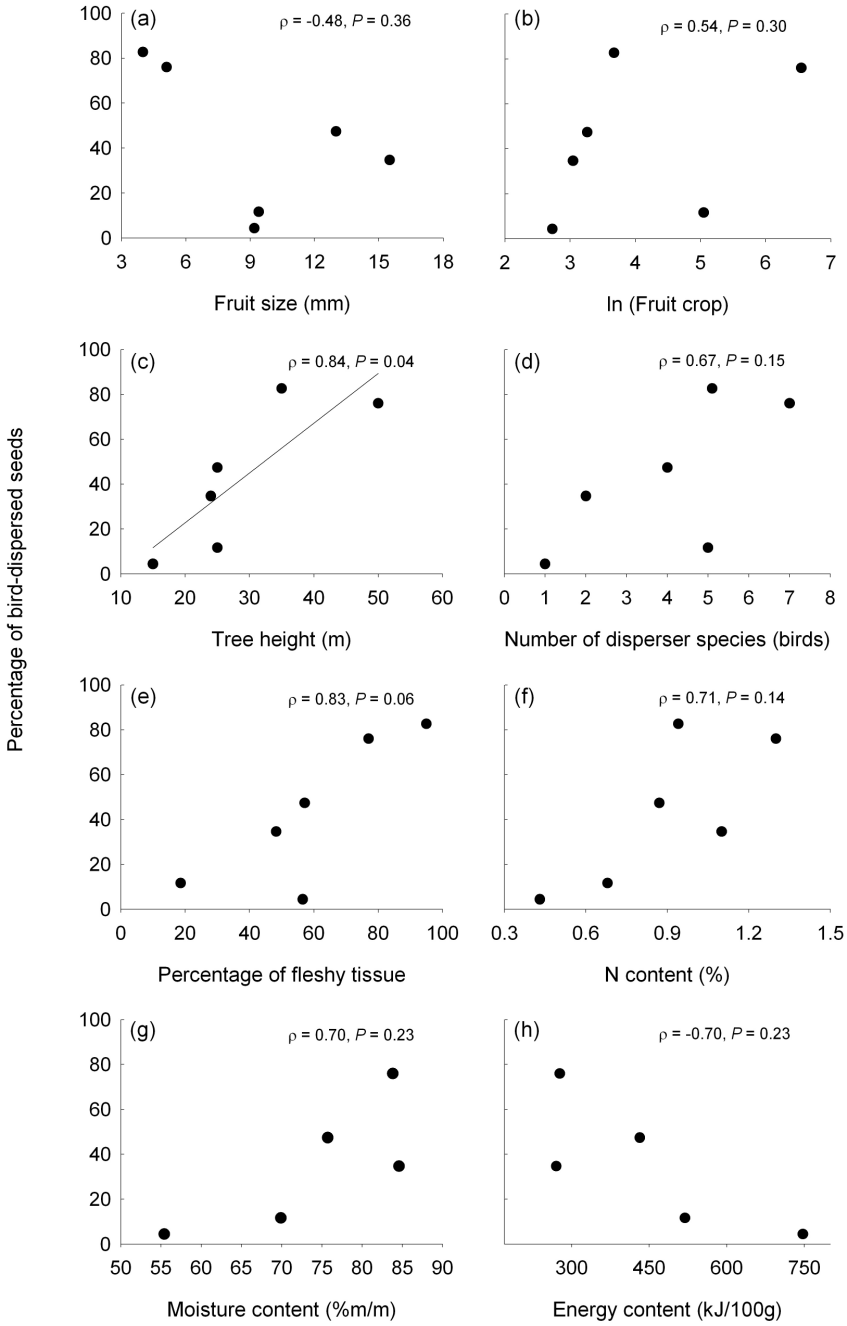


Figure 2. Correlations between percentage of the total fruit crop dispersed and different structural and nutritional characteristics of trees and fruits across the six species studied. Percentage of fleshy tissue were taken from Williams and Karl 1996 (*P. taxifolia*), Moles et al. 2000 (*D. cupressinum* seed weight), Dijkgraaf 2002 (*D. dacrydioides*, *E.dentatus*, *P. ferruginea* and *B. tawa*), Cottam et al. 2006 (*D. cupressinum* fruit wet weight). *Dacrydium cupressinum* is missing from (g) and (h) due to absence of data on the species. Spearman's rank correlation coefficients, ρ, and statistical significances are shown.

3.4.2 **Species composition at canopy and seed rain levels**

The seed rain of total seeds (whole fruits + bird-dispersed seeds + insect damaged + mammal damaged) was skewed towards conspecific canopies (80% total seeds), but all of the canopy species received seeds from heterospecific canopies (absent from above the seed traps), in different proportions (Fig. 3a). Note that for this figure (Fig. 3) only a subset of the seed traps (the ones with one canopy species above, n=28) and only the years with full information about whole fruits (2004-2010) were used. *Dacrycarpus dacrydioides* total seeds accounted for most of the seed rain (22 236 seeds) across the 28 seed traps, and also had the largest basal area of the trees above the seed traps (35% of total basal area sampled, n=7 trees, Fig. 3a). In spite of the different seed trap numbers (and therefore, different numbers of trees) the cumulative basal area sampled of *D. cupressinum*, *E. dentatus*, *P. ferruginea* and *B. tawa* was similar (14.2%, 13.7%, 15.5% and 13.4% , respectively). During this period (2004-2010) only 3 dispersed seeds of *E. dentatus* were collected. *Dacrydium cupressinum* and *B. tawa*, the two species at the two extremes of the fruit size range, presented similar numbers of total collected seeds (*D. cupressinum* = 731, *B. tawa* = 684), however, the number of dispersed *D. cupressinum* seeds collected in the seed traps (n = 352) was twice the number of *B. tawa* dispersed seeds (n=181) collected. Furthermore, 95% of the dispersed *D. cupressinum* seeds were found under heterospecific canopies. One third (31%) of total *D. dacrydioides* seeds were whole fruits (6 446 fruits), and its dominance in the total seed rain increased when only dispersed seeds are represented (87% of all dispersed seeds, Fig. 3b). Finally, a large proportion of the total *P. taxifolia* seed crop was collected under the canopy of *B. tawa* (Fig. 3a, 36%). This increased to the 43% of the *P. taxifolia* seeds when only dispersed seeds were represented (Fig. 3b).

The species composition in the canopy above all seed traps (n=55) was significantly different to the species composition in the bird-dispersed seed rain inside the seed traps (permutational MANOVA, Table 3). In the NMS, two convergent solutions were found after 12 runs (stress=0.17, Fig. 4). Two groups differing mainly in their statistical dispersion can be observed in the figure, with the seed traps characterized by bird-dispersed seed rain more close to each other than when characterized by canopy composition (Fig. 4). Same results (in terms of significant differences and increase in similarity) were obtained when the canopy composition was compared to total seed rain (period 2004-2010, Appendix 4).

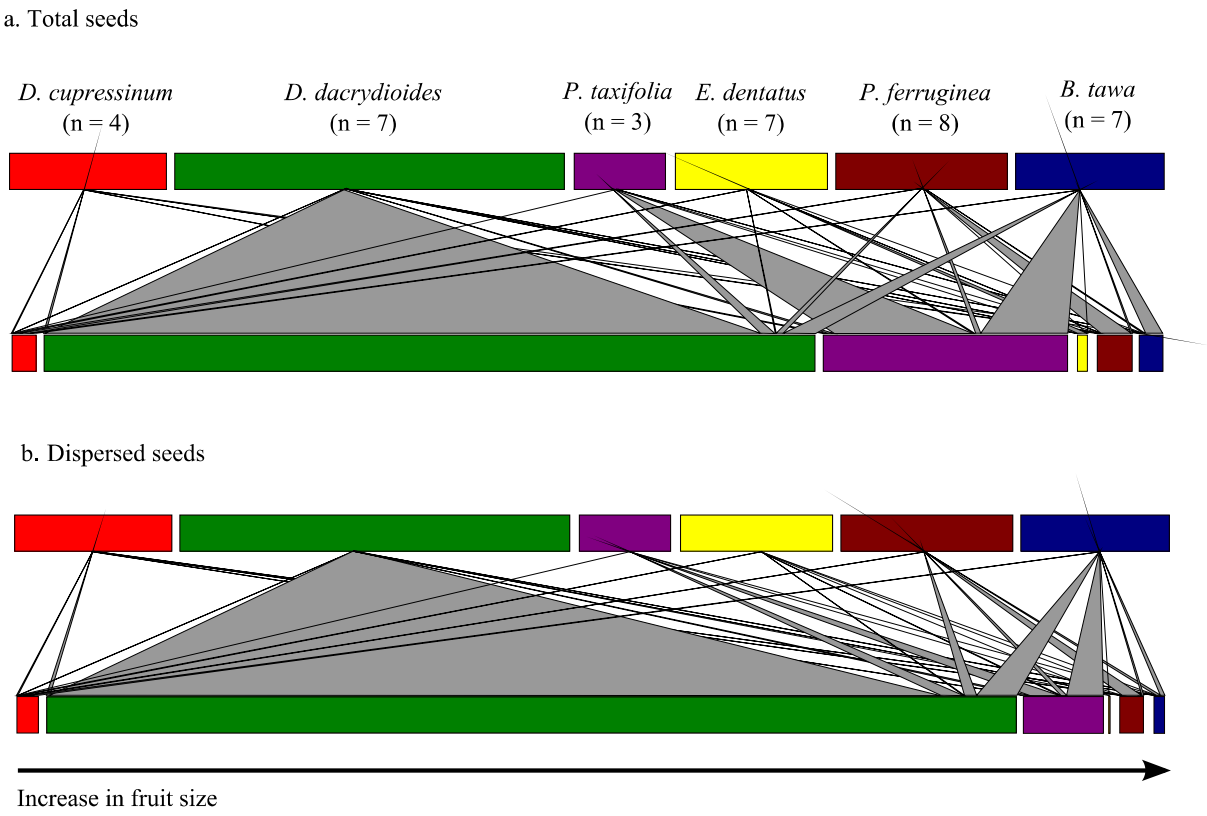


Figure 3. Proportions of basal areas and seed rain of (a) total seeds (n = 32,019) (b) dispersed seeds (17,647). 2004-2010. Only the subset of the seed traps with single canopies above was used for this representation (*D. cupressinum* n = 4, *D. dacrydioides* n = 7, *P. taxifolia* n = 3, *P. ferruginea* n = 8, *B. tawa* n = 6; total n=28). Top bars are identical in a and b, representing the proportion of basal area corresponding to each of the tree species in relation to the total basal area accumulated surrounding the 28 seed traps. Bottom bar represents the seed rain belonging to each species in the same color as top bar (same species both graphs). Arrow at the bottom of figure represents the direction of the increase in fruit size.

Table 3: Permutational MANOVA using distance matrices to test the dissimilarities between the seed rain of bird-dispersed seeds and tree canopy composition above the seed traps. Metric represents seed rain and canopy groups.

Source	d.f.	SS	MS	F	P	R^2
Metric	1	3.13	3.13	11.021	0.001	0.092
Residuals	108	30.71	0.28			
Total	109	30.84				

3.4.3 **Effects of tree canopies on seed rain**

The analysis of the relative importance of the different canopies on the seed rain revealed differences between the studied species in terms of their role as exporters and importers of seeds. I was not able to run the analysis on *E. dentatus* seeds, as I only collected 45 dispersed seeds during the 12 years sampled (Table 1). All the models used for model averaging with cumulative Akaike weights ≤0.95 are shown in Appendix 5, and the estimates for best model per plant species in Appendix 6. The effect of con-specifics on the seed rain of dispersed seeds was consistently positively high, except for *D. cupressinum* (Table 4 and Fig. 5). In general, the strongest effects were negative; however, several weak positive interactions between heterospecifics were found. All of the species were likely to fall under the canopy of at least one heterospecific species (Fig. 5). Cumulative Akaike weights indicated that all the heterospecific canopy species were strong predictors (either negative or positive) for *D. cupressinum* and *D. dacrydioides* seed rain ($w_+ > 0.50$, Table 4). The association of the seed rain of the three other species with heterospecific canopies was variable, dominated by smaller values of cumulative Akaike weights. In terms of the canopies, *E. dentatus* was a strong explanatory variable (with mainly negative effects, except for *D. cupressinum* seed rain) across the seed rain of the different species. Positive values of model averaged estimates represent seeds more likely to fall under specific canopies (Figs. 5a,5c,5e,5h and 5j), or canopies more likely to receive seeds from specific tree species (Figs. 5b, 5d, 5f, 5g, 5i and 5k). *Dacrydium cupressinum* seeds were more likely to fall under the canopy of large fruited trees (Fig. 5a). Overall, one small fruited species was more likely to export seeds to heterospecific canopies (Figs. 5a and 5c), but both received seeds from all heterospecific species studied (Figs. 5b and 5d). Large fruited trees did not receive nor send more seeds to other large fruited species (Figs. 5h-k). However, seed rain under the canopies of small-fruited species was similar to each other in species composition, with most of the coefficients for the parameters close to zero (Figs. 5b and 5d). In the same line, the seed rain under the canopy of large-fruited trees was similar, both receiving more seeds from *D. cupressinum* and conspecifics, followed by the second largest fruited tree in the study (Figs. 5i and 5k).

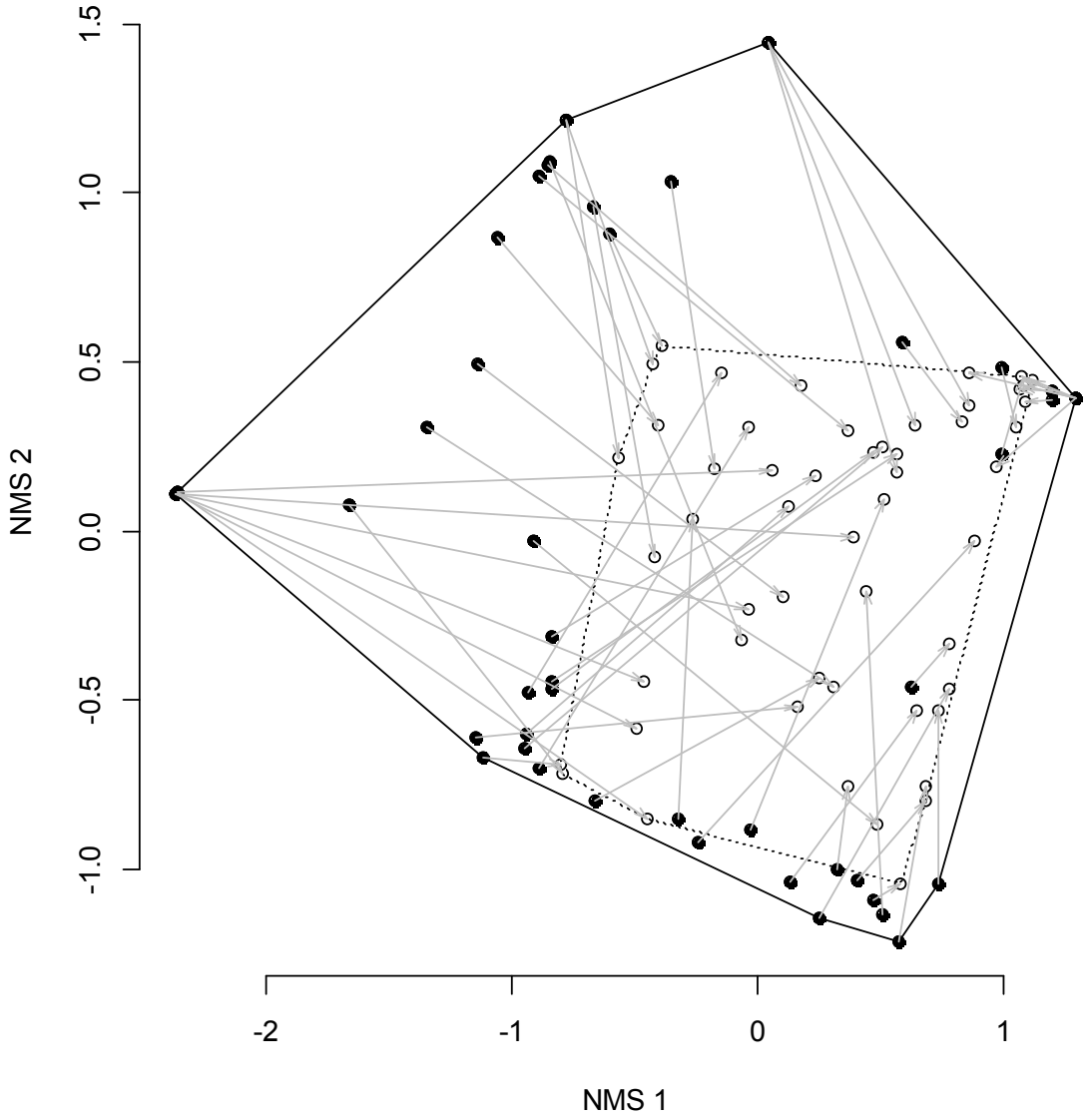


Figure 4. Non-metric multidimensional scaling (NMS) ordination for seed traps in Pelorus Bridge Scenic Reserve. Black dots represent seed traps characterized by canopy above them, white dots seed rain of bird-dispersed seeds collected inside seed traps (n=55 seed traps). Solid line encloses multi-space covered by canopy, dotted line encloses multi-space covered by seed rain. Stress = 0.1679.

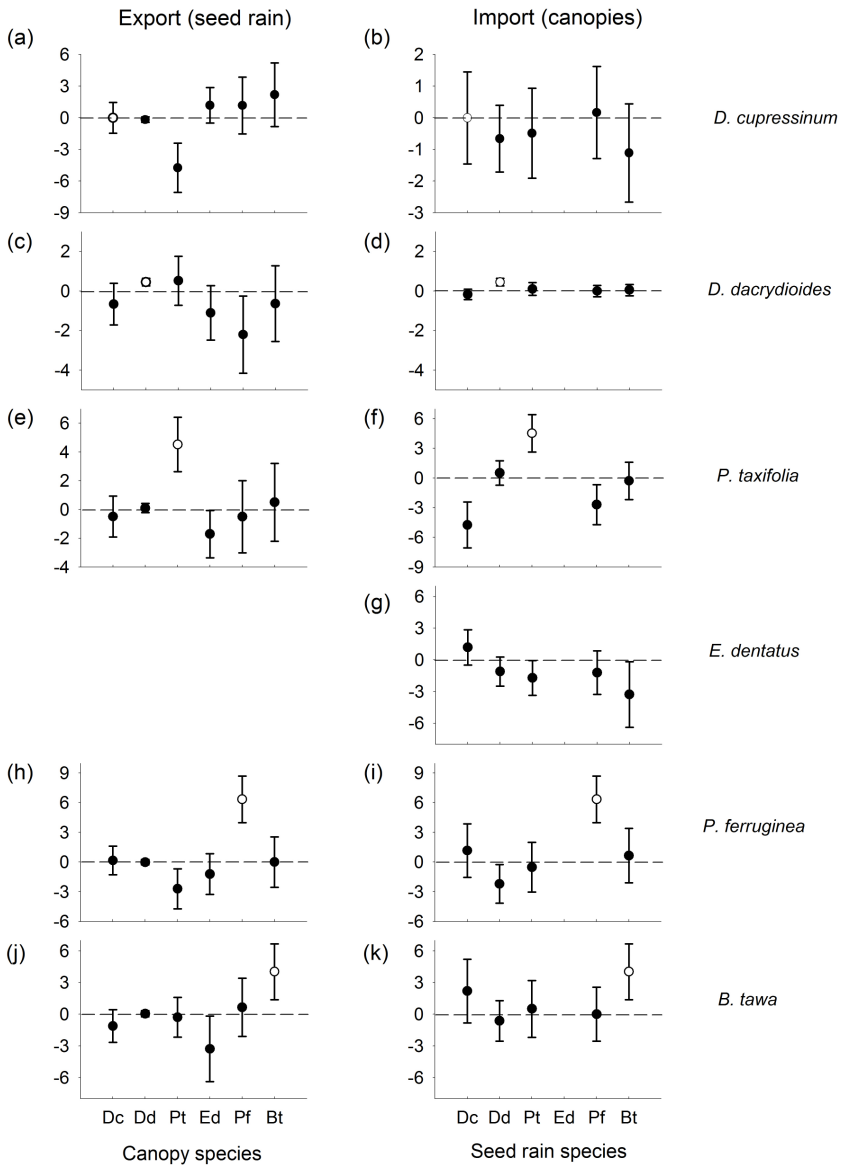


Figure 5. Model-averaged parameter estimates (± 95% confidence interval) representing the effects of canopy species on the seed rain of con- and hetero-specific species. Each panel represents one tree species either by its seed rain (left panels) or its canopy (right panels). Empty symbols represent effect of con-specific. Seed rain of *E. dentatus* was not sufficient to run statistical analysis. Seed fall data collected between 1986-1990 and 2004-2010 in Pelorus Bridge Scenic Reserve, New Zealand. Figures arranged from top to bottom and from left to right (x axis) by increasing in fruit size. Species codes are: Dc = *D. cupressinum*, Dd = *D. dacrydoides*, Pt = *P. taxifolia*, Ed = *E. dentatus*, Pf = *P. ferruginea* and Bt = *B. tawa*.

Table 4: Cumulative Akaike weights (w_+) of predictors in bird-dispersed seed rain models for species *D. cupressinum* (Dc), *D. dacrydioides* (Dc), *P.taxifolia* (Pt), *P. ferruginea* (Pf) and *B. tawa* (Bt). Seed fall for *E. dentatus* (Ed) was not sufficient to run statistical analysis. Seed fall data collected between 1986-1990 and 2004-2010 in Pelorus Bridge Scenic Reserve, New Zealand. $\hat{\beta}$ represents the parameter estimate in the models. Tree species are ordered from smallest (top-left) to largest (bottom-right) fruit size.

	Seed rain species											
	D. cupressinum		*D. dacrydioides*		*P. taxifolia*		*E. dentatus*		*P. ferruginea*		*B. tawa*	
Predictor (canopies)	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$
Dc	**0.27**	+/-	0.67	Negative	0.49	Negative	NA	NA	0.32	Positive	0.71	Negative
Dd	0.67	Negative	**1.00**	**Positive**	0.50	Positive	NA	NA	0.27	+/-	0.37	Positive
Pt	1.00	Negative	0.55	Positive	**1.00**	**Positive**	NA	NA	0.95	Negative	0.35	Negative
Ed	0.75	Positive	0.77	Negative	0.83	Negative	NA	NA	0.65	Negative	0.92	Negative
Pf	0.57	Positive	0.89	Negative	0.38	Negative	NA	NA	**1.00**	**Positive**	0.41	Positive
Bt	0.77	Positive	0.49	Negative	0.38	Positive	NA	NA	0.27	+/-	**0.98**	**Positive**

3.5 Discussion

In general, I found that dispersers are reducing the heterogeneity present in the canopy (where seeds are produced), homogenizing the seed rain, and increasing the similarity between the seed traps through seed dispersal. In general, seed fall is concentrated under the canopy of con-specific trees; however, birds are frequently dispersing the seeds under heterospecific canopies, presenting some positive associations with them, as much as when the canopies are single canopies above seed traps as when they are mixed. The character of importer/exporter of the trees was not necessarily given by fruit size only, but instead by the joint effects of different plant and fruits characteristics (fruit crop size, tree height, moisture content, etc). Some canopies attract a more diverse range of heterospecific seeds than others, so can be called "seed importers" (e.g. *B. tawa*, *D. cupressinum* and *D. dacrydioides*), as well as some seeds are moved more frequently to heterospecific canopies than others, as "seed exporters" (e.g. *D. cupressinum*). The increase in local homogeneity is probably a consequence of an increase in local diversity (propagule scale), creating new combinations of seeds on the ground (Chapter 2).

3.5.1 **Seed rain**

Ecologically similar species differed in the proportion of fruit crop dispersed across the seasons. The species with the smallest proportion of fruit crop dispersed towards heterospecific canopies was *D. dacrydioides* (7.3% of the total fruit crop, 8.2% of the dispersed-seeds), contrasting with *D. cupressinum*, from the same family and with a similar fruit size (i.e. similar disperser assemblage, 92.6% of its fruit crop and 95.2% of the dispersed seeds under heterospecific canopies). Previous research has found that species with larger fruit crop size and immersed in a fruiting neighborhood have higher fruit removal rates and higher total number of dispersed seeds (Takahashi and Kamitani, 2004; Carlo, 2005). This is concordant with my results, as the low proportion of *D. dacrydioide*s fruit crop dispersed is probably related to its very large fruit crop size (due to frugivore satiation, Hampe 2008), and was in fact, the species with the largest number of dispersed seeds collected. *Elaeocarpus dentatus* failed to be dispersed in Pelorus, with only three dispersed seeds collected between 2004 and 2010 (Fig. 2). The fruits of this tree are only consumed *by Hemiphaga novaeseelandiae* (New Zealand pigeon) in the study site (Table 1 and Kelly et al., 2010), where a suite of other fleshy fruited species is available during the same period. In a study in southern temperate forests of New Zealand, where the tree *Elaeocarpus hookerianus*, with fruits similar in color and shape to *E. dentatus*, but of smaller size, is present along with four of the six species I studied here, the fruits consumed by the NZ pigeon were 40.7% *D. cupressinum*, 30.3% *P. ferruginea*, 6.2% *D. dacrydioides* and 0.2% *P. taxifolia*, with no significant representation of *Elaeocarpus* in its diet (Warburton et al., 1992; O'Donnell and Dilks, 1994). However, there are reports of the NZ pigeon consuming *Elaeocarpus* fruits (D. García personal observation, T. Wyman personal communication). *Elaeocarpus dentatus* fruits have high carbohydrate content and low sugars, characteristics that make *E. dentatus* an unattractive species for dispersers (Appendix 2). It is possible that in Pelorus the overlap in the phenology between fleshy fruited species is more complete than in the other sites, giving the dispersers the chance to be more selective in terms of trees used as fruit sources.

3.5.2 **Community composition and homogenization of seed rain**

When I analyzed the seed rain inside seed traps located under the canopy of single trees none of the species presented exclusively con-specific seed rain. Even more, seeds from at least four of the five other species were found under the canopy of each of the species evaluated. These two results help explain the mechanisms for the homogenization in the seed rain of dispersed seeds. Previous studies have found a similar effect of seed dispersal on the seed fall patterns compared to the "source" composition (canopies). A recent study in a laurel forest at the Canary Islands compared the basal area composition and fruit fall composition among two sites. The authors found a weak relationship between canopy and fruit fall composition, with sites constituting two groups in the detrended correspondence analysis when they were

characterized by canopy composition, but not differing in the composition of the fleshy fruit biomass collected (Arévalo et al., 2007). The results of this larger scale (site scale) study support my findings at a smaller (seed trap) scale. Unfortunately, the study did not present both aspects of community composition in one figure nor carried out a statistical analysis to test these differences in the multivariated ordination. Moreover, as far as I know, my study is the first to test and find an explicit increase in spatial homogeneity in the seed rain composition compared to canopy composition, generated through seed dispersal.

When the movement of the seed dispersers is intense, and no particular preferred plant species food source is found, one can expect a homogenization in the seed rain. In my study all of the species were successful in attracting seeds from at least one heterospecific canopy, and this was also represented in the data of seed rain under single canopies. Clark et al. (2004) found that in a tropical semi-deciduous forest in Cameroon large birds were creating spatially contagious seed dispersal and the composition of non-conspecific seed rain under the canopy of bird-dispersed trees was more similar between trees than to the composition of non-conspecific seed rain under the canopy of monkey- or wind-dispersed trees. The effects of the increase in local diversity are that, as the number of individuals (seeds, in my case) moving between the "communities" (seed traps) increases, homogenization increases, decreasing beta diversity (Cadotte, 2006). One of the possible caveats of my study is that as it is based on seed rain sampled under the canopy of fruiting trees, and on birds as the main seed dispersers, my results might be applicable only to this type of system. For example, Blendinger et al. (2011) found that the bird-mediated seed rain inside of seed traps placed in four types of microsites (three fruiting species and randomly selected sites) differed in seed abundance and composition between microsites, especially with randomly selected microsites (Blendinger et al., 2011). However, these differences were non-consistent across the different statistical approaches they used. Nonetheless, the seed rain of seeds from fleshy fruited species in open sites and under the canopy of non-fruiting trees is also generated through animal-mediated seed dispersal, and will necessarily have a representation of the neighboring plants carrying fleshy fruits, and therefore will as well increase the homogenization of the seed rain on the ground.

3.5.3 **Effects of tree canopies on seed rain**

In my study I evaluated the associations between the seed rain patterns of six bird-dispersed tree species and the canopy composition. Bird-mediated seed rain was generally not random between canopies, with the seed rain biased towards conspecifics, one species standing out as a strong "exporter" of its seeds to heterospecific larger-fruited canopies (*D. cupressinum*), another species receiving more heterospecific seeds than the others, therefore "importing" seeds (*B. tawa*), and several weak positive interactions between heterospecifics.

A large part of what determines frugivore activity in trees is species-specific to the birds. Bird choices on what tree to visit, how much time to stay, or where to fly to after feeding are all disperser species-specific (Herrera et al., 1994; García, 2001; Levey and Martínez del Rio, 2001; Martínez et al., 2008). Structural elements such as fruit crop size, level of aggregation of the fruiting trees, and fruiting neighborhood can influence tree selection, fruit removal rates and total number of seeds removed by birds (Carlo and Morales, 2008; García et al., 2010). Fruit crop size has been frequently described as the most important determinant of bird attraction and hence seed arrival (Sallabanks, 1993; Takahashi and Kamitani, 2004; Saracco et al., 2005; Carlo and Morales, 2008), particularly of conspecific seeds (Blendinger et al., 2011). Fruiting neighborhood also can affect fruit-removal rates, through an indirect effect on the behavior of the dispersers (Saracco et al., 2005; Carlo and Morales, 2008). The presence of conspecifics in the immediate surroundings can reduce per-tree removal rates, but the presence of heterospecific fruiting trees can facilitate the arrival of frugivores, increasing fruit removal rates for the focal tree (Saracco et al., 2005) and increasing the arrival of heterospecific seeds under the canopy (Blendinger et al., 2011). In my study, the percentage of total fruit crop that was collected as bird-dispersed seeds was not correlated with fruit crop size, but there was a strong tendency to a correlation with the number of disperser species and fruit size, probably weaken by the small sample size (n=6) . Unfortunately, I don't have information on the fruiting neighborhood (year to year) nor levels of tree aggregation in my site, or canopy structure of the species sampled. These elements could be also playing an important role in the seed fall patterns in this temperate forest and this is an open area for future research.

In New Zealand temperate forests, an extra element plays an important role on seed dispersal. As the original frugivore avifauna has been reduced in 50% on the mainland (mainly the largest frugivores, Anderson *et al.* 2006), and novel exotic species have been human- or self-introduced (five species, Anderson et al. 2006) in present times differences in fruit size determine important differences in species richness of the disperser assemblages that can consume, and move the seeds in the landscape (Kelly *et al.* 2010 and Table 1). The species richness of the disperser assemblage will be important in terms of their diversity of foraging and resting behavior, and will also influence the abundance of dispersers for the different tree species. From my results I can infer that the number of dispersers was not limiting for small fruited trees (*D. cupressinum* and *D. dacrydioides*), as they presented the highest proportions of total fruit crop dispersed (even for the species with largest fruit crop, *D. dacrydioides*). These two species are also the tallest trees of the six species studied (Table 1), The foraging behavior of the two largest seed dispersers in the study site, *P. novaeseelandiae* (tui) and *H. novaeseelandiae* (New Zealand pigeon) is biased towards the upper tiers of the forest canopy (Warburton et al., 1992). Tree height was positively

correlated with the proportion of fruit crop dispersed, and it has been previously postulated as a factor that could determine frugivores choice, with contrasting results (Slocum and Horvitz, 2000; Flörchinger et al., 2010). Medium- and large-fruited trees had smaller proportions of fruit crop removed relative to small-fruited trees; however, medium sized fruits were relatively less dispersed than large fruits. If there is a preference of birds for larger fruits with higher proportion of seed/pulp, but the number of dispersers is limiting for medium and large fruits, I could then expect to find a higher proportion of *P. ferruginea* and *B. tawa* fruit crops as dispersed seeds, as the frugivores would be selectively foraging on larger fruits. Previous literature has identified *P. ferruginea* fruits as one of the preferred food items of the NZ pigeon (McEwen, 1978; Clout and Hay, 1989; O'Donnell and Dilks, 1994), therefore very likely to receive seeds from heterospecific species consumed by this species. The NZ pigeon has been described as a consumer of at least 70 species of fleshy fruits (Clout and Hay, 1989) and the only recorded disperser of *E. dentatus* seeds (Kelly et al., 2010). The pigeon is also the main consumer of *B. tawa* fruit due to its fruit size, therefore, the high importance of *E. dentatus*, *P. ferruginea* and *B. tawa* as importers of *D. cupressinum* seeds could be a consequence of the feeding and resting behavior of the practically sole disperser of of these three large-fruited trees. Even more, the effect of the canopy of *P. ferruginea* and *B. tawa* on heterospecific seed rain was similar, suggesting common disperser assemblages between them. I found the same with the small-fruited trees *D. cupressinum* and *D. dacrydioides*. Common seed deposition patterns for trees with common dispersers have been previously reported for other bird-dispersed species (Clark et al., 2004). The community-level consequences of this pattern will depend on the presence of density-dependent mortality processes, as I would expect to find synergistic effects of multi-specific seed rain under the canopy of species acting as "seed importers", due to different seed predation rates found on some of the species here studied (Chapters 4 and 5).

3.5.4 **Concluding remarks**

My results show that bird-mediated seed dispersal reduces the heterogeneity present in the canopy composition above the forest floor at the propagule stage. It also gives insights on the different roles different plant species can play in this change, and how birds can consistently move seeds towards heterospecific canopies through seed dispersal. However, this is only the beginning of the recruitment process, and the effect of this biased seed rain under heterospecific canopies is still to be seen in future research on this system. The effects of multispecific seed rain on the recruitment are also an open area for new research. The heterogeneity of the environment, in terms of biotic and abiotic factors, will modify the homogeneity in the dispersed-seeds template (Cavallero et al., in press; Grubb, 1977). Environmental filtering and intra- and inter-specific competition will prevent the successful recruitment of many of the seeds. The reduction in available seeds and seedlings for adult replacement through density-dependent

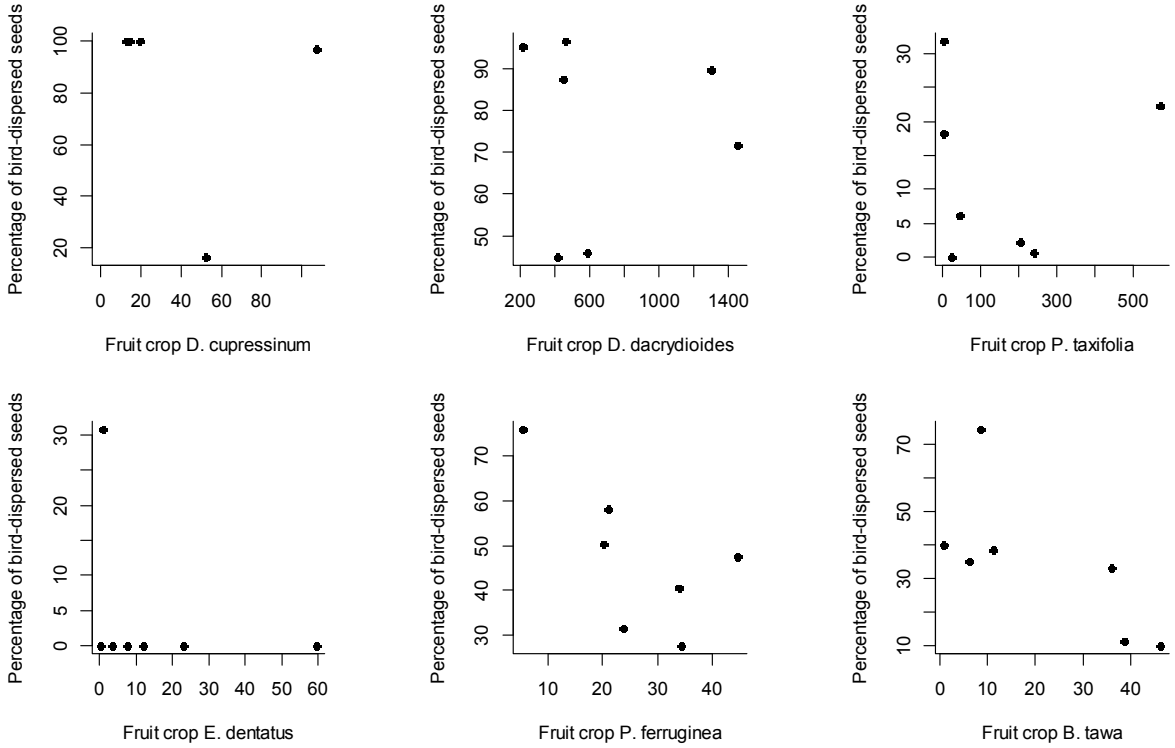
processes as seed predation and pathogens attacks has been extensively demonstrated in tropical forests, and it is very likely that is also present in temperate forests (Packer and Clay 2000, Wotton and Kelly 2011, Chapter 5). Differentiation in the regeneration niche will allow environmental filters to reduce the successful recruitment for seedlings emerging in environments too different from where conspecific saplings are found (Cavallero et al. in press; Grubb, 1977). At an inter-specific scale the same process of differentiation in the regeneration niche will determine if an adult plant is replaced by an individual from the same or a different species, finally increasing the community diversity (Grubb, 1977).

3.6 Appendix 1

Seed traps used during this study. Seed trap model on the ground (green mesh) was used for collections between 1986 and 1990, and then was replaced by the standing seed trap model for collections 2004-2010. Photo taken by Dave Kelly.

3.7 Appendix 2

Intraspecific relationship between fruit crop size (per species, x axis) and percentage of it collected as bird-dispersed seeds (y axis).



3.8 Appendix 3

Nutritional contents of the fleshy tissue for five of the six species used in this study. Fruits of *D. cupressinum* were not available at the time of the analysis, therefore, information available from other studies was used (Cottam et al., 2006; Cottam, 2010).^ values for whole fruit. Spearman's rank correlation coefficients ρ between the average percentage of dispersed seeds (bottom row) and each element are provided. No values with statistical significance $P < 0.05$ were found, · = 0.05 < P < 0.1.

		Tree species						
Test	Units	*Dc*	*D d*	*Pt*	*Ed*	*Pf*	*Bt*	*ρ*
Nitrogen	%	0.94	1.30	0.68	0.43	0.87	1.10	0.71
Phosphorus	%	0.001	0.22	0.22	0.06	0.12	0.18	-0.17
Moisture	%m/m		83.80	69.90	55.40	75.70	84.60	0.83·
Fat content	g/100g	2.4^	0.84	1.44	0.29	2.00	1.09	0.60
Protein	g/100g		1.45	1.51	1.35	1.75	1.12	0.30
Ash	%m/m	5.6^	0.96	1.30	0.96	1.24	0.82	0.38
Fructose	%m/m		1.72	8.08	0.00	3.57	2.51	0.10
Glucose	%m/m		2.80	3.95	<0.02	4.63	3.13	0.30
Other sugars	%m/m		0.00	-0.03		0.05	0.18	0.20
Total sugars		4.25^	4.52	12.00	<0.05	8.25	5.82	-0.08
Carbohydrates	g/100g		13.00	25.90	42.00	19.30	12.40	0.03
Energy	kJ/100g		277	519	747	432	270	-0.07
Sodium	mg/100g	16.3	7.07	3.15	4.24	17.90	<2	0.60
Acid-Detergent Fibre	%		28	10	24	16	20	0.30
Cellulose	%		10	5	11	6	11	-0.20
Acid-Detergent Lignin	%		18	5	12	9	10	0.3
Condensed Tannins (catechin equiv.)	%		<0.2	0.2	<0.2	<0.2	<0.2	NA
Total Phenolics (tannic acid equiv.)	%		<0.5	0.7	1.2	<0.5	0.9	NA
Average percentage of bird-dispersed seeds		82.6	76.0	11.6	4.4	47.4	34.7	

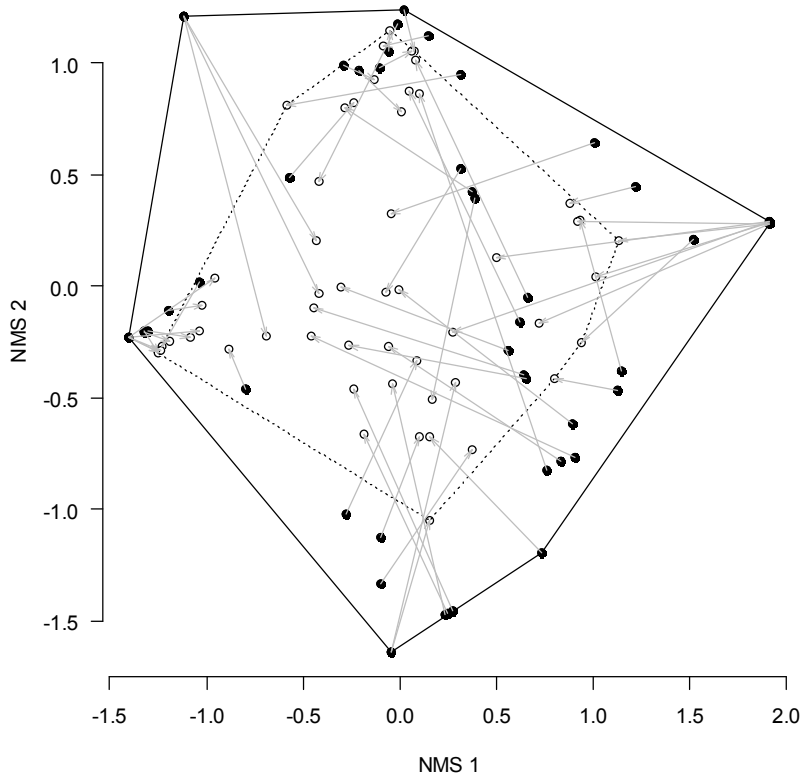
Information on moisture for *P. taxifolia* taken from Williams and Karl (1996) and Moles et al.(2000)

3.9 Appendix 4

(a) Results for a permutational MANOVA using distance matrices to test the dissimilarities between the total seed rain (whole fruits + bird-dispersed seeds) and tree canopy composition above the seed traps. Metric represents seed rain and canopy groups.

Source	d.f.	SS	MS	F	P	R^2
Metric	1	1.506	1.51	4.671	0.001	0.041
Residuals	108	34.825	0.32			
Total	109	36.331				

(b) Non-metric multidimensional scaling (NMS) ordination for seed traps in Pelorus Bridge Scenic Reserve. Black dots represent seed traps characterized by canopy above them, white dots seed rain of all seeds (whole fruits + bird-dispersed seeds) collected inside seed traps (n=55 seed traps). Solid line encloses multi-space covered by canopy; dotted line encloses multi-space covered by seed rain. Stress = 0.1970



3.10 Appendix 5

Model selection for canopy influence in the seed rain of bird dispersed seeds (glmm), only models with cumulative Akaike weights ≤0.95 are shown. ΔAICc is used to rank the models. $L(g_i|x)$= likelihood of a model g_i given the data x; w_i = Akaike weight; ER = evidence ratio. Codes for the species are: Dc = *Dacrydium cuppresinum*, Pt = *Prumnopitys taxifolia*, Ed = *Elaeocarpus dentatus*, Pf = *P. ferruginea*, Bt = *Beilschmiedia tawa*.

Species	Model	K	log ($\mathcal{L}$)	AICc	ΔAICc	$\mathcal{L}(g_i\|x)$	w_i	ER	Cum. w_i
Dc	Dd + Pt + Ed + Pf + Bt	9	-612.2	1242.7	0.00	1.00	0.18		0.18
	Pt + Ed + Pf + Bt	8	-613.6	1243.4	0.69	0.71	0.13	1.41	0.32
	Dd + Pt + Ed + Bt	8	-613.8	1243.9	1.20	0.55	0.10	1.82	0.42
	Dc + Dd + Pt + Ed + Pf + Bt	10	-612.2	1244.8	2.06	0.36	0.07	2.81	0.48
	Dc + Pt + Ed + Pf + Bt	9	-613.5	1245.4	2.68	0.26	0.05	3.82	0.53
	Dd + Pt + Bt	7	-615.6	1245.4	2.69	0.26	0.05	3.83	0.58
	Pt + Ed + Bt	7	-615.7	1245.6	2.93	0.23	0.04	4.33	0.62
	Dd + P	6	-616.8	1245.7	3.04	0.22	0.04	4.58	0.66
	Dd + Pt + Ed	7	-615.8	1245.8	3.10	0.21	0.04	4.70	0.70
	Dc + Dd + Pt + Ed + Bt	9	-613.8	1245.8	3.12	0.21	0.04	4.77	0.74
	Dd + Pt + Pf + Bt	8	-615.0	1246.3	3.58	0.17	0.03	5.99	0.77
	Dd + Pt + Ed + Pf	8	-615.2	1246.7	3.98	0.14	0.03	7.31	0.80
	Dc + Dd + Pt + Bt	8	-615.5	1247.2	4.47	0.11	0.02	9.37	0.82
	Dd + Pt + Pf	7	-616.5	1247.3	4.58	0.10	0.02	9.87	0.83
	Dc + Pt + Ed + Bt	8	-615.7	1247.7	4.97	0.08	0.02	11.98	0.85
	Dc + Dd + Pt	7	-616.8	1247.8	5.09	0.08	0.01	12.73	0.86
	Dc + Dd + Pt + Ed	8	-615.8	1247.8	5.12	0.08	0.01	12.96	0.88
	Pt + Bt	6	-617.9	1247.9	5.16	0.08	0.01	13.20	0.89
	Pt + Ed	6	-617.9	1248.0	5.28	0.07	0.01	14.03	0.91
	Pt + Pf + Bt	7	-617.0	1248.2	5.47	0.06	0.01	15.39	0.92
	Dc + Dd + Pt + Pf + Bt	9	-615.0	1248.2	5.51	0.06	0.01	15.71	0.93
	Pt + Ed + Pf	7	-617.0	1248.3	5.57	0.06	0.01	16.16	0.94
	Pt	5	-619.2	1248.5	5.76	0.06	0.01	17.82	0.95
Dd	Dc + Dd + Ed + Pf + Bt	9	-1948.5	3915.4	0.00	1.00	0.15		0.15
	Dc + Dd + Ed + Pf	8	-1949.7	3915.7	0.30	0.86	0.13	1.16	0.29
	Dc + Dd + Pt + Ed + Pf	9	-1948.8	3915.9	0.54	0.76	0.12	1.31	0.41
	Dc + Dd + Pt + Ed + Pf + Bt	10	-1947.8	3916.0	0.64	0.72	0.11	1.38	0.52
	Dd + Pt + Ed + Pf + Bt	9	-1949.5	3917.2	1.84	0.40	0.06	2.51	0.58

Species	Model	K	log ($\mathcal{L}$)	AICc	ΔAICc	$\mathcal{L}(g_i\|x)$	w_i	ER	Cum. w_i
	Dd + Ed + Pf + Bt	8	-1950.6	3917.4	2.08	0.35	0.05	2.83	0.64
	Dd + Pt + Ed + Pf	8	-1950.7	3917.7	2.32	0.31	0.05	3.19	0.68
	Dc + Dd + Pt + Pf	8	-1950.8	3917.9	2.54	0.28	0.04	3.57	0.73
	Dd + Pt + Pf	7	-1952.1	3918.4	3.03	0.22	0.03	4.55	0.76
	Dd + Ed + Pf	7	-1952.2	3918.6	3.27	0.19	0.03	5.13	0.79
	Dc + Dd + Pt + Pf + Bt	9	-1950.4	3919.1	3.78	0.15	0.02	6.62	0.81
	Dd + Pt + Pf + Bt	8	-1951.5	3919.1	3.78	0.15	0.02	6.63	0.84
	Dc + Dd + Pf	7	-1952.5	3919.2	3.85	0.15	0.02	6.86	0.86
	Dd + Pt	6	-1953.8	3919.7	4.37	0.11	0.02	8.88	0.88
	Dd + Pt + Ed	7	-1953.0	3920.2	4.85	0.09	0.01	11.31	0.89
	Dc + Dd + Pf + Bt	8	-1952.0	3920.3	4.90	0.09	0.01	11.60	0.91
	Dc + Dd + Pt + Ed	8	-1952.1	3920.4	5.04	0.08	0.01	12.44	0.92
	Dc + Dd + Pt	7	-1953.1	3920.4	5.05	0.08	0.01	12.50	0.93
	Dd + Pf	6	-1954.3	3920.7	5.33	0.07	0.01	14.35	0.94
	Dd + Pf + Bt	7	-1953.4	3921.0	5.67	0.06	0.01	17.04	0.95
Pt	Dd + Pt + Ed	6	-1086.7	2185.4	0.00	1.00	0.10		0.10
	Pt + Ed	5	-1087.8	2185.7	0.28	0.87	0.08	1.15	0.18
	Dc + Pt + Ed	6	-1087.0	2186.1	0.64	0.73	0.07	1.38	0.25
	Dc + Pt + Ed + Pf	7	-1086.0	2186.1	0.66	0.72	0.07	1.39	0.32
	Dc + Dd + Pt + Ed	7	-1086.1	2186.4	1.00	0.61	0.06	1.65	0.37
	0 + Pt + Ed + Pf	6	-1087.2	2186.5	1.06	0.59	0.06	1.70	0.43
	Dc + Pt + Ed + Bt	7	-1086.2	2186.5	1.10	0.58	0.05	1.74	0.48
	Dc + Dd + Pt + Ed + Bt	8	-1085.3	2186.7	1.32	0.52	0.05	1.93	0.53
	Dc + Pt + Ed + Pf + Bt	8	-1085.3	2186.8	1.34	0.51	0.05	1.95	0.58
	Dd + Pt + Ed + Pf	7	-1086.3	2186.8	1.36	0.51	0.05	1.98	0.63
	Dd + Pt + Ed + Bt	7	-1086.3	2186.8	1.36	0.51	0.05	1.98	0.68
	Dc + Dd + Pt + Ed + Pf	8	-1085.5	2187.2	1.80	0.41	0.04	2.45	0.72
	0 + Pt + Ed + Bt	6	-1087.6	2187.4	1.96	0.38	0.04	2.66	0.75
	Dd + Pt	5	-1088.8	2187.8	2.32	0.31	0.03	3.19	0.78
	Dc + Dd + Pt + Ed + Pf + Bt	9	-1084.8	2187.8	2.37	0.31	0.03	3.28	0.81
	Pt + Ed + Pf + Bt	7	-1087.1	2188.4	2.92	0.23	0.02	4.32	0.83
	Dd + Pt + Ed + Pf + Bt	8	-1086.1	2188.4	3.00	0.22	0.02	4.47	0.85
	Dd + Pt + Bt	6	-1088.3	2188.6	3.20	0.20	0.02	4.95	0.87
	Pt	4	-1090.4	2188.9	3.47	0.18	0.02	5.67	0.89
	Dc + Dd + Pt + Bt	7	-1087.5	2189.2	3.78	0.15	0.01	6.63	0.91

Species	Model	K	log ($\mathcal{L}$)	AICc	ΔAICc	$\mathcal{L}(g_i\|x)$	w_i	ER	Cum. w_i
	Dc + Dd + Pt	6	-1088.6	2189.3	3.84	0.15	0.01	6.82	0.92
	Dd + Pt + Pf	6	-1088.8	2189.6	4.20	0.12	0.01	8.17	0.93
	Dc + Pt	5	-1089.9	2189.9	4.42	0.11	0.01	9.12	0.94
	Dc + Pt + Bt	6	-1089.0	2190.1	4.66	0.10	0.01	10.28	0.95
Pf*	Pt + Ed + Pf	6	-761.9	1536.0	0.00	1.00	0.24		0.24
	Pt + Pf	5	-763.7	1537.5	1.47	0.48	0.11	2.09	0.35
	Dc + Pt + Ed + Pf	7	-761.7	1537.6	1.67	0.43	0.10	2.30	0.45
	Dd + Pt + Ed + Pf	7	-761.9	1537.9	1.95	0.38	0.09	2.65	0.54
	Pt + Ed + Pf + Bt	7	-761.9	1538.0	2.04	0.36	0.08	2.77	0.62
	Dc + Pt + Pf	6	-763.3	1538.8	2.82	0.24	0.06	4.10	0.68
	Pt + Pf + Bt	6	-763.6	1539.4	3.44	0.18	0.04	5.60	0.72
	Dd + Pt + Pf	6	-763.7	1539.5	3.51	0.17	0.04	5.78	0.76
	Dc + Pt + Ed + Pf + Bt	8	-761.7	1539.7	3.67	0.16	0.04	6.28	0.80
	Dc + Dd + Pt + Ed + Pf	8	-761.7	1539.7	3.69	0.16	0.04	6.31	0.84
	Dd + Pt + Ed + Pf + Bt	8	-761.9	1540.0	3.98	0.14	0.03	7.32	0.87
	Dc + Dd + Pt + Pf	7	-763.3	1540.8	4.84	0.09	0.02	11.24	0.89
	Dc + Pt + Pf + Bt	7	-763.3	1540.8	4.86	0.09	0.02	11.35	0.91
	Dd + Pt + Pf + Bt	7	-763.6	1541.5	5.49	0.06	0.02	15.54	0.93
	Dc + Dd + Pt + Ed + Pf + Bt	9	-761.7	1541.7	5.69	0.06	0.01	17.19	0.94
	Pf	4	-767.3	1542.6	6.58	0.04	0.01	26.87	0.95
Bt	Dc + Ed + Bt	6	-472.5	957.1	0.00	1.00	0.16		0.16
	Dc + Pt + Ed + Bt	7	-471.8	957.9	0.77	0.68	0.11	1.47	0.27
	Dc + Ed + Pf + Bt	7	-471.9	957.9	0.84	0.66	0.11	1.52	0.38
	Dc + Dd + Ed + Bt	7	-472.1	958.5	1.36	0.51	0.08	1.97	0.46
	Dc + Dd + Ed + Pf + Bt	8	-471.3	958.8	1.74	0.42	0.07	2.39	0.53
	Dc + Pt + Ed + Pf + Bt	8	-471.5	959.2	2.09	0.35	0.06	2.84	0.58
	Ed + Bt	5	-474.6	959.3	2.17	0.34	0.05	2.96	0.64
	Dc + Dd + Pt + Ed + Bt	8	-471.7	959.5	2.43	0.30	0.05	3.37	0.68
	Ed + Pf + Bt	6	-473.8	959.8	2.73	0.26	0.04	3.92	0.73
	Dd + Ed + Pf + Bt	7	-473.0	960.1	3.00	0.22	0.04	4.47	0.76
	Dd + Ed + Bt	6	-474.0	960.2	3.06	0.22	0.03	4.61	0.80
	Pt + Ed + Bt	6	-474.2	960.5	3.37	0.19	0.03	5.39	0.83
	Dc + Dd + Pt + Ed + Pf + Bt	9	-471.1	960.5	3.39	0.18	0.03	5.43	0.86
	Pt + Ed + Pf + Bt	7	-473.6	961.4	4.33	0.11	0.02	8.73	0.87
	Dd + Pt + Ed + Bt	7	-473.7	961.7	4.56	0.10	0.02	9.78	0.89

Species	Model	K	log ($\mathcal{L}$)	AICc	ΔAICc	$\mathcal{L}(g_i\|x)$	w_i	ER	Cum. w_i
	Dd + Pt + Ed + Pf + Bt	8	-472.9	962.0	4.92	0.09	0.01	11.69	0.90
	Dc + Bt	5	-476.3	962.7	5.65	0.06	0.01	16.86	0.91
	Dc + Pf + Bt	6	-475.4	962.9	5.84	0.05	0.01	18.50	0.92
	Dc + Dd + Pf + Bt	7	-474.4	962.9	5.84	0.05	0.01	18.58	0.93
	Dd + Pf + Bt	6	-475.7	963.5	6.37	0.04	0.01	24.17	0.94
	Dc + Dd + Bt	6	-475.7	963.5	6.37	0.04	0.01	24.22	0.94
	Pf + Bt	5	-477.0	964.1	7.02	0.03	0.00	33.51	0.95

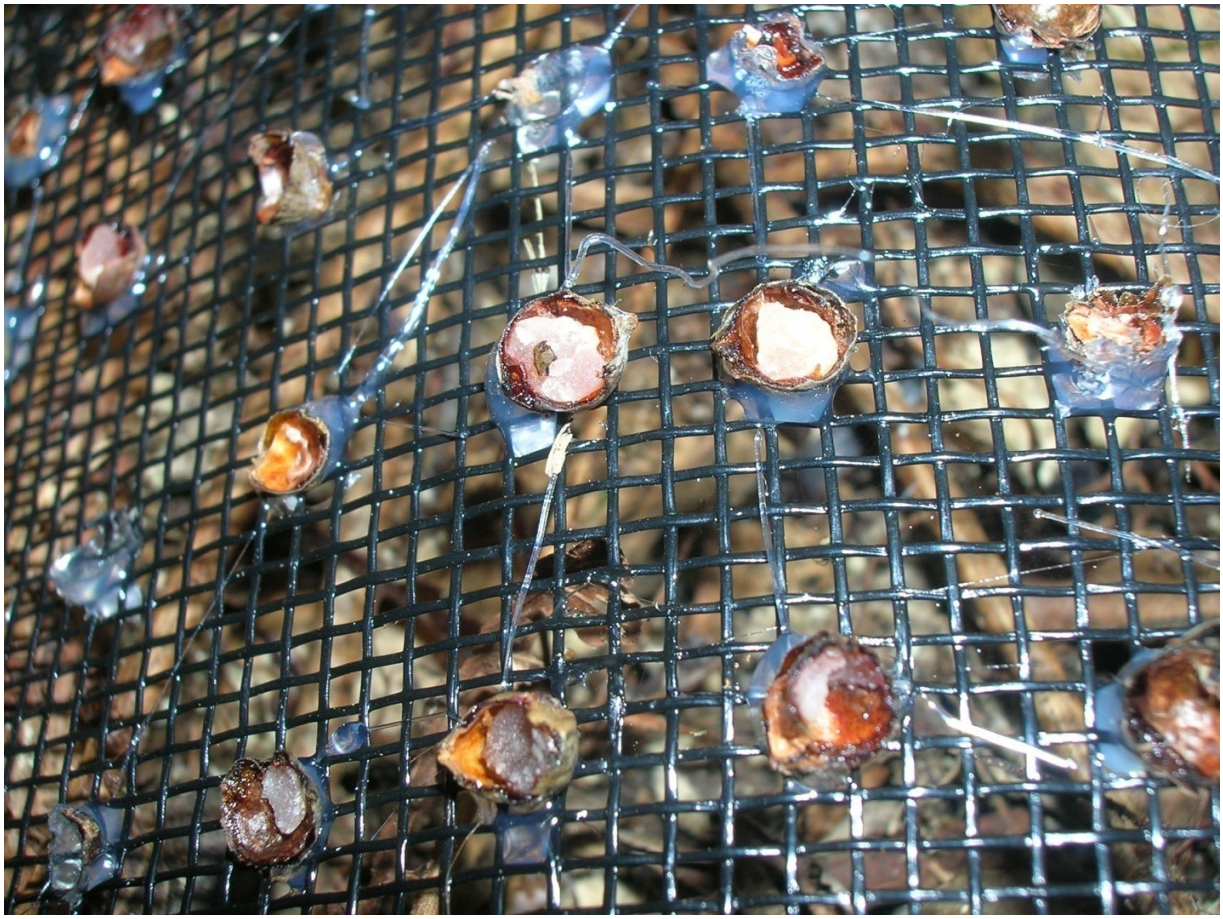
*model with Dc + Ed + Bt failed

3.11 Appendix 6

Best model estimates per species and errors (between brackets). Best model was chosen as the one with the lowest number of parameters (K) whose $\Delta AICc < 2$.

Seeds	Family	K	α	ZIpar	Intercept	Dc	Dd	Pt	Ed	Pf	Bt	R^2
D. cupressinum	ZINB	8	0.36	0.58	0.37 (0.38)			-4.21 (1.09)	1.91 (0.80)	2.47 (1.27)	3.36 (1.46)	0.002
D. dacrydioides	ZINB1	8	366	$1e^{-06}$	3.88 (0.16)	-1.15 (0.50)	0.41 (0.08)		-1.52 (0.64)	-2.67 (0.90)		0.17
P. taxifolia	NB	5	0.11	-	1.01 (0.18)			4.47 (0.88)	-2.06 (0.81)			0.05
P. ferruginea	NB	5	0.86	-	-0.83 (0.19)			-2.67 (1.0)		6.53 (1.14)		0.13
B. tawa	NB	6	0.19	-	-1.10 (0.21)	-1.61 (0.77)			-3.63 (1.53)		4.15 (1.27)	0.03

CHAPTER 4



Dacrycarpus dacrydioides (kahikatea) seeds eaten, probably by mice

4 Effects of seed density and introduced mammals on post-dispersal seed predation, germination and survival

4.1 Abstract

1. New Zealand forests hold a suite of exotic seed and seedling mammalian predators. House mice, rats and brushtail possums consume the seeds, fruits and seedlings of a variety of plant species, reducing their recruitment and potentially altering forest regeneration. Ungulates such as deer also consume seedlings on the forest floor, but this usually affects individuals more than 10 cm tall. Shifts in the environmental filters, seed predators and herbivores across ontogeny can differentially affect plant recruitment.

2. Plant species vary in their attractiveness to predators, and the density of the resource (seeds, seedlings) can alter the behaviour of the predators. This can modify the outcome of the interaction between plant propagules and predators, increasing or decreasing plant survival. To date, most of the research on the effects of seed and seedling predators in New Zealand forests has been carried out on species with particular characteristics (e.g. masting species, large seeded species), but the effects of density *per se* (independent from the distance from conspecifics) or seed size have not been evaluated.

3. I investigated the effects of seed and seedling density on seed predation, seedling emergence and seedling survival to 12 months of five tree species in a New Zealand temperate forest of the South Island. I used a factorial design of density with and without cages to exclude seed and seedling predators. I expected to find different seed predation rates between species (with different seed sizes) and between seed densities in uncaged depots. I did not expect to find differences in seedling survival between species when these were protected from exotic predators, but decreased survival when predator access was permitted and at high seed densities.

4. Using an information-theoretic approach I identified the main predictors of seed predation, seedling emergence and seedling survival. Seed predation increased with seed size, and it was higher at high density only for the largest-seeded species. Seed predation in small-seeded species was negligible, although density effects were important in one of them.

5. Access of seed and seedling predators to the propagules was the main factor affecting seedling emergence and seedling survival. Abiotic variables were important for germination and seedling survival of the two small-seeded species, but only biotic predictors (mammalian exclosure and density) were important for medium and large-seeded species.

6. The long-term impacts of exotic seed and seedling predators for canopy tree recruitment in New Zealand temperate forests are still too recent to be evident. My results demonstrate the importance of

these animals on propagule survival of five species in a New Zealand forest. This type of study helps understand the interactions between native plant and exotic animal species, and can improve my understanding of the present state of New Zealand indigenous forests.

4.2 Introduction

New Zealand plants evolved in the absence of mammalian seed predators and herbivores, with only three species of mammals in its forests, all of them bats (King, 2005). With the arrival of Maori people 800 years ago, and the British colonizers in the 1800s, completely new guilds of mammals (browsers, granivores, onmivores) were introduced to New Zealand. The number of mammalian species in New Zealand increased from three to 36 species (Atkinson and Cameron, 1993). Many of these species have become invasive species, and have impacted New Zealand ecosystems irreversibly (Atkinson and Cameron, 1993; Towns and Ballantine, 1993; Wilson, 2004). For example, the introduction of rats has caused the extinction of several bird species, and rats are likely to be responsible for the presumed extinction of one of the three endemic mammals, *Mystacina robusta*, the Greater short-tailed bat (Wilson, 2004). Mutualisms such as pollination and seed dispersal have been reduced through the extinction of several pollinator and frugivorous species, and reduction of the populations of remaining species (Clout and Hay, 1989; Kelly et al., 2010). In the specific case of seed dispersal, this has left the dispersal of fleshy fruited species relying on a few flying frugivorous species (including exotic birds) and some opportunistic ground birds (Kelly et al., 2010; Wotton and Kelly, 2011). Thanks to conservation efforts some of the frugivores are currently recovering their population numbers (Innes et al., 2010). Studies of the impact of the introduced mammals on the vegetation in New Zealand forests through seed predation and herbivory have shown that the long term consequences occur across multiple geographic and ecological scales and are extremely difficult to predict (Veblen and Stewart, 1982; Wardle et al., 2001; Grant-Hoffman et al., 2010; Mason et al., 2010). It is, therefore, important to understand the effects that the reduction of seed dispersers and the presence of novel seed predators and herbivores can have on New Zealand native plant species (Wotton and Kelly, 2011). Species-specific short-term experiments based on factorial designs can contribute empirically and experimentally with data to inform models that attempt to predict the outcome of these new interactions between native plants and introduced mammals.

The effects of seed and seedling predators on New Zealand plant species have been studied in different New Zealand ecosystems and forest types (Bellingham et al. 2010; Bellingham & Allan 2003; Ruscoe et al. 2004; Wilson et al. 2003, 2007, 2006; and others). Seed predation on the ground is exerted mainly by the house mouse (*Mus musculus*) and rats (*Rattus rattus* - ship rat, *R. norvegicus* - Norway rat,

R. exulans – kiore; this last one has been extirpated from most of the mainland and multiple offshore islands, King 2005) (Beveridge, 1964; Daniel, 1973; Innes, 1979). Brushtail possums (*Trichosurus vulpecula*) also consume the fruits of at least 65 plant species (King, 2005), but most of the seeds are destroyed and only seeds smaller than 10 mm can remain viable after consumption by this species (Dungan and Norton, 2003; Williams, 2003). Seed predation rates can go from very low (mean of 11 species = 9.8%, Moles & Drake 1999) to moderate numbers (10 - 30% in two large-seeded species, Wotton & Kelly 2011). The effects of exotic seed and seedling predators can be mediated by variation in seed and seedling density, that arises from seed dispersal processes and differential survival of seedlings (Chapters 2 and 3; Clark, Poulsen, & Levey 2012; Hautier et al. 2010; Wotton & Kelly 2011). House mice and rats are capable of detecting changes in resource density, increasing their abundance in neighborhoods with high density of food (Wilson et al., 2007), and even responding at population scale after masting events of species as *Dacrycarpus dacrydioides* (Podocarpaceae) and *Nothofagus* spp. (Nothofagaceae) (Ruscoe et al., 2004; Harper, 2005; McQueen and Lawrence, 2008). Multiple records show that rats and brushtail possums are also important seedling predators (Beveridge & Daniel 1965; Campbell 1978; Grant-Hoffman & Barboza 2010; Wilson et al. 2003; among others). Podocarp seedling mortality due to attack by Norway rats can reach up to 20% in winter in Mokoia Island (Rotorua Lake, Beveridge & Daniel 1965). Whenever any of these groups (rats or possums) are present at high abundances in a site, seedling numbers can be reduced drastically. For example, when rats were dominant, the number of true seedlings (seedlings with true leaves) was reduced to 27.5% of the abundance of seedlings in plots where rats and possums were excluded (Wilson et al., 2003). Effects of browsing by ungulates have been found to be evident on seedlings ≥ 10 cm tall, and can affect a wide range of species, although they do select species select their target according to the palatability of the plant (Wilson et al., 2006).

Seed density and seed size are two factors that are often expected to interact with seed and seedling success, as density-dependent processes as predation are likely to be affected by seed size. Increased seed density (e.g. under the parent or from clumped seed dispersal) may increase seed and seedling predation rates (Janzen, 1970, 1971; Kwit et al., 2004). However, this can be modulated by seed size, as larger seeds can be conspicuous no matter at what density they are, but small seeds can decrease their survival through increased visibility (Hulme and Borelli, 1999). It is also possible that increasing seed density for large seeds increase mortality (Willson and Whelan, 1990) or not change seed predation rates determined by seed size (Alcántara et al., 2000). Recently emerged seedlings can compete for nutrients, light or moisture, reducing per-capita survival if they are immersed in con- or hetero-specific clumps, although these mechanisms are infrequent (Terborgh, 2012). The increased visibility of the

seedling at high density can attract seedling herbivores more often, or enhance the arrival of generalist or host-specific pathogens (Alvarez-Loayza and Terborgh, 2011). As results of studies evaluating the influence of density and seed size on propagule survival are mixed, species-specific experiments are needed to understand the particular cases.

In this chapter my aim is to measure the effects of seed density and seed size on seed predation, establishment and seedling survival of different seed-sized plant species. To do this I set a seed predation experiment deploying seeds in the field of five species: *Pseudopanax arboreus*, *Coprosma robusta* (both small-seeded), *Dacrycarpus dacrydioides* (medium-sized seed), *Prumnopitys ferruginea* and *Beilschmiedia tawa* (both large-seeded) at two densities, and followed their survival for 80 days. I also set up a seed germination and recruitment experiment, and followed seedling survival for one year from sowing for the same species listed above except *P. ferruginea*. Both experiments were carried out in a temperate podocarp-broadleaved forest in Marlborough district, South Island of New Zealand.

Specifically, I expect:

(1) Seed predation to be higher at high seed densities and for large-seeded species, and almost no seed predation in small-seeded species (i.e. seed size x density interaction). As large-seeded species in my study have been often found eaten in the study site, I expect larger densities to increase seed visibility, and therefore, to increase seed predation.

(2) Seed survival and germination to be affected by seed density, reducing seedling emergence for large-seeded species at high densities, and not changing it for medium and small seeded species (seed size x density interaction). For small-seeded species high densities won't increase seed predation rates, therefore, germination won't be affected by density. For large-seeded species seeds will suffer high seed predation and therefore reduced germination at high densities.

(3) Seedling survival to be affected equally in all species by seed density, with higher survival at low densities (density main effect). Seedlings emerged in dense clumps might be subjected to increase attacks by pathogens and/or predators, independent from seed size.

4.3 Methods

4.3.1 **Study site**

The research was carried out in Blue Duck Scientific Reserve (42°14' S, 173°47' E, 400 m elevation), Marlborough district, South Island of New Zealand. This Reserve contains a rare remnant of mature mixed podocarp forest (Norton and Courtney, 2000). The climate is oceanic cool-temperate characterized by warm summers and mild winters, with a summer (January) average minimum temperature of 6.6° C,

and maximum of 28.8° C, and in winter (July) min temperature of 2.5° C and max of 18.8° C (New Zealand Meteorological Service, 2012). Annual rainfall is moderate with 1400-1600 mm (Breese et al. 1986). Soil pH ranges between 6.9 and 7.2 in the upper 150 mm of soil; this, together with other soil characteristics, is expected to produce moderate to high fertility for the plants (Hurst 2002).

The Reserve presents variation in altitude, from the base of the hill at approximately 250 m.a.s.l. to 415 m.a.s.l. Low altitudes of the Reserve have high abundance of *Nothofagus solandri* (Nothofagaceae) as tongues along spurs and clumps up to 350 m altitude, beneath emergent podocarps (Norton and Courtney, 2000). A relatively dense subcanopy of angiosperms is also present at low altitude, with *Pseudopanax arboreus*, *P. crassifolius* (Araliaceae), *Carpodetus serratus* (Rousseaceae), *Melicytus ramiflorus* (Violaceae) and *Pittosporum eugenioides* (Pittosporaceae) (Norton and Courtney, 2000). Shrubs such as *Coprosma* spp. and tree ferns are also abundant. However, most of the Reserve is dominated by mixed podocarp-broadleaf forest. The dominant species in the reserve are emergent *Dacrydium cupressinum*, *Prumnopitys taxifolia* and *Podocarpus totara* (all Podocarpaceae). Also present are *Dacrycarpus dacrydioides* and less abundant *Prumnopitys ferruginea*, but both of them sparser than the other podocarps. The canopy of these species reaches 22 m. A lower angiosperm canopy (12-15 m) is also present in most of the Reserve with *M. ramiflorus*, *Elaeocarpus dentatus* (Elaeocarpaceae), *Hedycarya arborea* (Monimiaceae) and *Alectryon excelsus* (Sapindaceae). Several small patches of *Beilschmiedia tawa* (Lauraceae), are scattered through the Reserve, where *B. tawa* is locally dominant in the angiosperm canopy (Norton and Courtney, 2000).

Exotic mammalian seed and seedling predators present at Blue Duck are the house mouse (*Mus musculus*), ship rat (*Rattus rattus*), the Norway rat (*R. norvegicus*), brushtail possum (*Trichosurus vulpecula)* and very likely feral pigs (*Sus scrofa*). Red deer *Cervus elaphus* also consume seedlings and young shoots of trees. Native invertebrate herbivores are also present. There is no evidence of seed caching by mammals in New Zealand (Wilson et al., 2007), however it is possible that for some species whose seeds remain viable in the soil for several years (e.g. *P. ferruginea*) seed removal could promote regeneration in hidden places where ship rats might take the seeds for safer consumption (Wilson et al., 2003).

4.3.2 **Study species**

In this study I selected five plant species present in the Reserve, comprising a variety of seed sizes and potential attractiveness to seed and seedling predators (Table 1). *Coprosma robusta* and *Pseudopanax arboreus* are present throughout the Reserve, but concentrated in the lower altitudes where *Nothofagus solandri* is present with an open canopy. *Dacrycarpus dacrydioides* and *P. ferruginea* are present throughout the Reserve while *Beilschmiedia tawa* is above 300 m.a.s.l.

Table 1. Characteristics of the species studied. Dashes in seed length and seed diameter represent ranges. Same initial seed densities were used in both experiments.

Species	Family	Seed size (mm)		Initial seed density	
		Length	Diameter	High	Low
P. arboreus	Araliaceae	2.9 - 4.5	2.9 - 4.5*	100	9
C. robusta	Rubiaceae	4.2 - 6.5	2.0 - 3.0	100	9
D. dacrydioides	Podocarpaceae	4.5 - 5.8	4.37	100	12
P. ferruginea	Podocarpaceae	11.0 - 17.0	11.0	30	5
B. tawa	Lauraceae	22.0 - 30.0	11.4	18	4

Plant families from Salmon (1980). Seed sizes are from Webb & Simpson (2001), this study and Kelly et al. (2010). *No data was found for *P. arboreus* seed diameter; however, as the seed is round I used the same values as in length.

Post-dispersal seed predation on *P. arboreus* and *C. robusta* has not been previously assessed in New Zealand (for some information on pre-dispersal seed predation on *Coprosma* see Sullivan, Burrows, & Dugdale 1995). *Dacrycarpus dacrydioides* is predated by rats (ship rat and kiore-*Rattus exulans*, the latter absent from the study site) and probably mice (Beveridge, 1964; Campbell, 1978; Ruscoe et al., 2004). *Prumnopitys ferruginea* fruits and seeds are predated by all rat species present in New Zealand (ship rat, kiore and Norway rat) (Grant-Hoffman and Barboza, 2010). Post-dispersal seed predation on *Beilschmiedia tawa* is by invertebrate insects and mammals. The larvae of the moth *Cryptaspasma querula* consume the endosperm of the seeds on the forest floor (Beveridge, 1964), eating also the embryo in most of the cases. Vertebrates like the brushtail possums and feral pigs also consume the fruits from the forest floor (Knowles and Beveridge, 1982).

4.3.3 **Experimental design**

I carried out two independent experiments to evaluate the effects of seed density on seed predation, germination and seedling survival in four to five plant species in Blue Duck. The aim of the first experiment was to quantify the effects of seed density on post-dispersal seed predation of five woody species (Table 1). The second experiment was designed to evaluate the effects of seed density and

mammal access on seedling emergence and seedling survival. I did this experiment on four of the five species above, excluding *P. ferruginea* because its germination is extremely slow, starting after 18 months and continuing for seven years (Clout & Tilley 1992; Kelly et al. 2010, D. Kelly and J. Ladley unpublished data). All the seeds used for these experiments were collected at the study site as close as possible to the beginning of the experiments. Seeds were collected as whole fruits directly from the trees (*C. robusta* and *P. arboreus*) or on the ground when the fruits were too high in the canopy to collect (*D. dacrydioides*, *P. ferruginea* and *B. tawa*). Fruits were collected from at least ten different trees of each species. Fleshy tissue was manually removed and seeds were processed at the University of Canterbury glasshouse facilities for the different experiments.

Experimental units were displayed in ten experimental stations in the Reserve, starting from the base of the hill (247 m.a.s.l.) and ending at the top (415 m.a.s.l.) to encompass the whole range of microhabitats in the Reserve where the species are naturally found. Each station had one set of seed predation units (five species, each one at high and low seed densities, n = 10) and one set of recruitment units (four species, each at high and low densities, caged and open, n = 16).

4.3.3.1 Seed predation

Each seed predation station had the five species at high and low densities (Fig. 1, Table 1). Seeds were offered simultaneously to seed predators in the field. Seeds from a particular species at a particular density were homogeneously distributed on and glued to a black plastic mesh (1-mm pore) 13 x 13 cm with the use of a low odour, rainproof thermoplastic glue (see Herrera *et al.* 1994; Alcantara *et al.* 2000; García, Obeso, & Martínez 2005 for a similar method). Seeds were glued to the mesh to minimize seed losses due to bad weather. Meshes were placed at each station in the field, separated by at least 5 meters between each other. Species and densities (species 1 to 5, and densities high and low) were randomly assigned to each point, and meshes fixed to the ground with two metal pegs (Fig. 2). The experiment was started on 30 July 2009, and seed predation was monitored at 13, 30 and 80 days. Seeds were considered as predated if (1) there were empty seed coats or eaten husks on the mesh or next to it (Fig. 2g, bottom left of the photo) (2) it was gnawed on the mesh (Fig. 2c), (3) it was missing from the mesh and not found next to it (however in these cases the possibility of secondary dispersal is discussed when appropriated, Wilson *et al.* 2003).

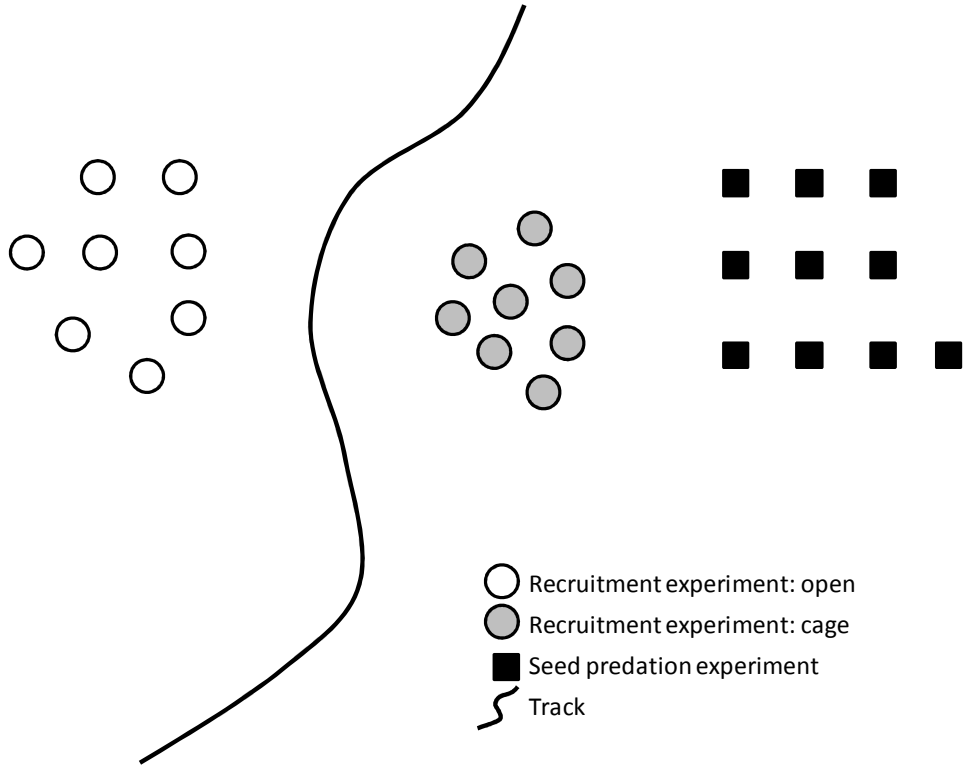


Figure 1. Design of the sampling stations with the seed predation and recruitment experiments. Seed predation experiment units (black squares, n = 10) consisted of five species at low and high seed densities (five x two), glued to a square plastic mesh and open to predator access. The units for the recruitment experiment (open and grey circles) were separated by 5 m. It consisted of one set of open units (white circles, n=8, with each unit holding seeds of one of four species at high or low seed densities (densities not represented here) and one set of caged units (grey circles, n = 8) to prevent mammal access.

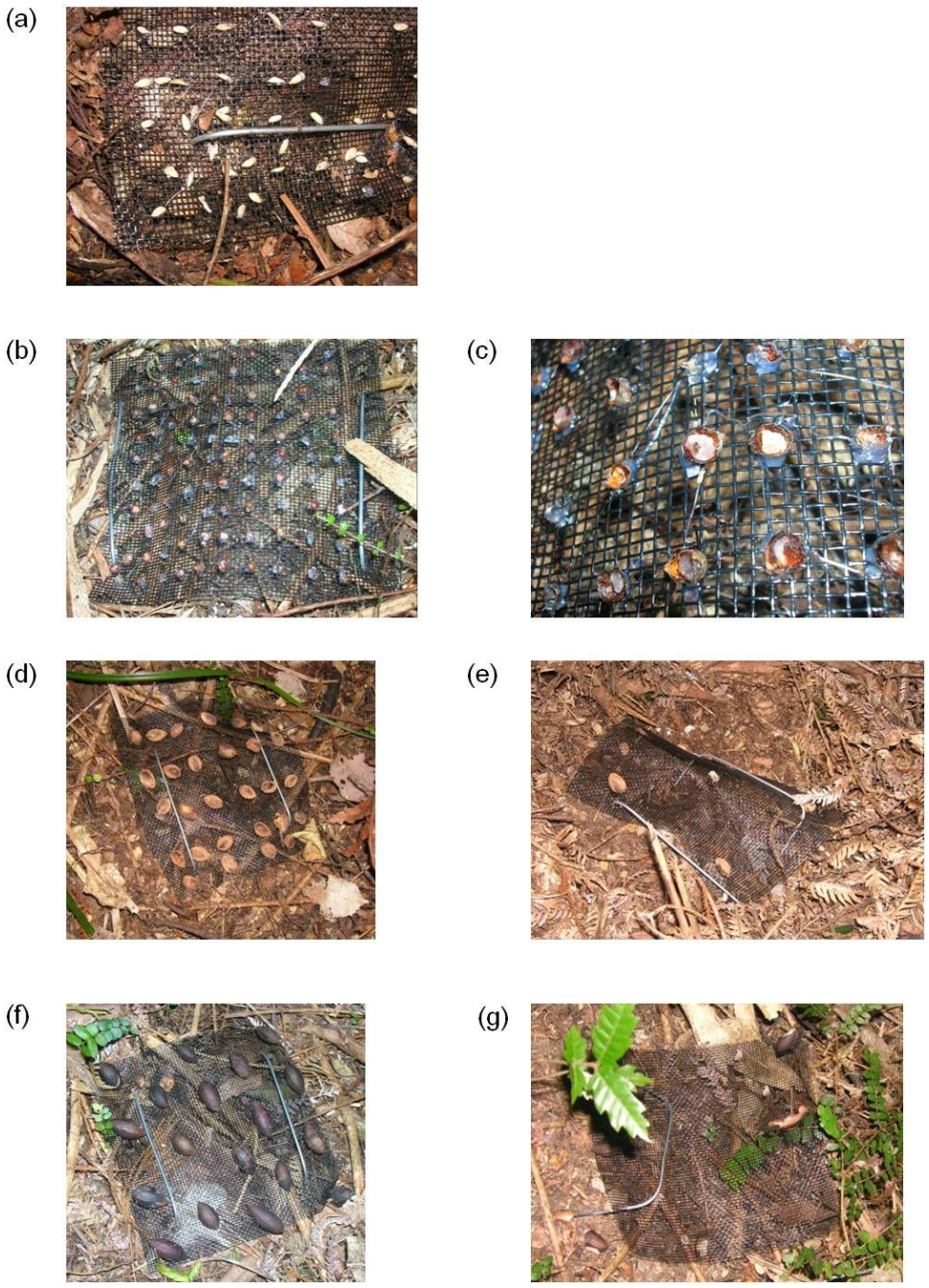


Figure 2. Seed predation experimental units. (a) high density *C. robusta*; (b) high density *D. dacrydioides*; (c) eaten seeds on the mesh with high seed density of *D. dacrydioides*; (d) high density *P. ferruginea*; (e) seed predators disturbed unit of low density *P. ferruginea* (note that seeds stay on the mesh unless they are actively taken by a predator); (f) high density *B. tawa*; (g) low density *B. tawa*. Note eaten seeds in (b),(c) and (g).

4.3.3.2 Recruitment experiment: germination and seedling survival

For the recruitment experiment seeds were prevented from rolling away and being lost by placing them inside open-topped and open-bottomed polycarbonate tubes 30 mm high and 120 mm diameter. Tubes were fixed to the ground using two wire pegs. To exclude vertebrate seed and seedling predators from some of the tubes I constructed cages made of welded galvanized mesh with 5 mm aperture, 20 cm diameter and 30 cm high. For each species two open tubes and two caged tubes were placed in each sampling station (4 species x 2 densities= 8 tubes per type of exclosure). All species and densities were randomly assigned to particular tube locations. Leaf litter was placed in the tubes on top of the seeds to minimize increased attraction to seeds coming from augmented conspicuousness and to prevent seeds drying out. Tubes were monitored for 12 months; I recorded seedling emergence and seedling survival for each unit. In this experiment seedling emergence refers to seeds that survived seed predation (seed survival) and germinated (seed germination), and therefore, "seedling emergence" effects include also the effects of seed predation. Seeds were sowed on 29 July 2009. I monitored for germination at frequent intervals, starting on the 3rd of November, with no presence of germination. Germination was recorded on the 17th of December 2009, monitored monthly until February 2010 and in July 2010 (one year from sowing). At each visit litter from beside the cage was placed into the tubes, to emulate the natural litterfall on seeds in the "open" treatment.

Seed germination and seedling survival can also be affected abiotic variables as soil pH, depth of organic soil and others. I therefore measured the altitude of each sampling station with a portable GPS (Garmin 60C Sx), and verified on a topographic map. Soil pH at sampling station level was also measured in three mineral soil samples of 15 cm deep and 5.8 cm wide taken using a soil core sampler near the cages area on 1 September 2010, and mixed in the laboratory. The samples were then oven dried at 30º C for seven days, sieved through 3 mm mesh size, mixed in a 1.2 vol:vol soil to water suspension for 30 seconds, after 10 min settling the pH was determined on the supernatant with a portable pHmeter (PHM201, meterlab) (Aravena et al., 2002; McCay and McCay, 2008). The depth of organic soil was measured on 1 September 2010 next to each tube on each station in mm using a shovel and a metallic ruler. Ground and canopy cover (shading) were visually estimated for each tube in ordinal categories of 0-25, 25-50, 50-75 and 75-100, with absolute values of 0 and 100 in the extremes. Ground cover was estimated as the percentage of soil covered with organic matter (leaf litter and vegetation) in a 1 x 1 m plot and canopy cover as the percentage of covered sky above 1.30 m.

The final number of replicates for seedling emergence was 10, except for *P. arboreus* cage-low, *C. robusta* cage-low, *D. dacrydioides* open-high and *B. tawa* open-high n = 9; *P. arboreus* open-high n = 8, due to damage from falling trees or disturbances from predators (e.g. deer trip over, cage opened). Final

number of replicates for seedling survival varied, as only tubes where some germination was recorded were used for its calculation. Numbers as follows: *C. robusta* cage-low, *D. dacrydioides* both cages, open-high, *B. tawa* cage-high and open-high n = 9; *P. arboreus* open-high, *C. robusta* open-high, *B. tawa* open-low n = 8; *P. arboreus* both cages and open-low n = 6; *C. robusta* cage-high and open-low n = 5; *B. tawa* cage-low n = 4; *D. dacrydioides* open-low n = 2.

4.3.4 **Data analysis**

4.3.4.1 Seed predation

To evaluate the effects of time, seed density and the interaction between both on seed predation for the different species evaluated I ran generalized linear mixed effects models (GLMMs). GLMMs are able to deal with non-normal and overdispersed data, frequent cases in ecological data (Bolker et al., 2009). It also allows specifying the effects of repeated measures on the response variable through the inclusion of a random effects predictor accounting for the experimental design. As my response variable was the proportion of surviving seeds at different times I used a binomial error distribution with logit link for all models. When data was overdispersed I included an extra random effects predictor accounting for the individual-level variability (Bates et al., 2011). For the analysis I used package lme4 version 0.999375-42 (Bates et al., 2011) in R software version 2.14.1 (R Development Core Team, 2011). I analyzed the data separately for each species using model selection with an information-theoretic approach (Burnham and Anderson, 2002). For more information on the basis of the procedure see section 3.3.2 in Chapter 3. As my interest was focused on the two main predictors (seed density and time) as well as on the interaction between them, I constructed the models of interest prior to the analysis. However, this resulted in the candidate set of models including all possible models (n = 5 models, including also an only random effects model to estimate the variance not explained by the predictors). I therefore used the function "dredge" in MuMIn package version 1.7.7 (Barton, 2012). For each model in the set I calculated AICc, ΔAICc, w_i and the evidence ratio. ΔAICc is the difference between the model with the lowest AICc in the set and the model under scrutiny; therefore, ΔAICc is the first criterion used to rank the models. w_i is the Akaike weight of the model, it represents the probability of each model in the set being the best model ($\sum w_{i\ model\ set} = 1$). Finally, evidence ratios (ER) are relative to the other models in the set, and give a quantification of the weight of the evidence for each of the models in the set in a more intuitive manner (Burnham and Anderson, 2002). The goodness of fit for the "best" model for each species was evaluated through the calculation of a pseudo-R-squared based on the likelihood ratio available in MuMIn package through function r.squaredLR (Barton, 2012). This coefficient can be interpreted as the proportion of the

variance explained by the model. All the analyses were done in R software version 2.14.1 (R Development Core Team, 2011).

4.3.4.2 Germination and seedling survival

To evaluate the effects of seed density and the exclosure of mammalian predators on germination and seedling survival I used generalized linear mixed models (GLMMs). Analysis was done per plant species. Prior to running the analyses I evaluated the correlation between covariates (pH, altitude, organic soil, canopy cover and ground cover). Correlated covariates were re-evaluated, and one of them eliminated if it was not supplying extra information.

I calculated the seedling emergence across all dates, and seedling survival (number of final seedlings / seedling emergence) after one year, in both cases using a binomial error distribution with logit link. I also included the sampling station as a random effects variable, and, when data were overdispersed I included an individual-level random effects parameter (Bates et al., 2011). An information theoretic approach (Burnham and Anderson, 2002) was used to select the main predictors of seedling emergence and final seedling survival in these four species. I defined a priori a set of ten candidate models, including the effects of density and exclosure together and separated, as well as the presence of covariates (Table 2). Following the same principles as in the previous section, I calculated AICc, ΔAICc, w_i and the evidence ratio using the package AICcmodavg (Mazerolle, 2012). After the first analysis on a subset of candidate models, and to overcome model uncertainty in the cases were the best AICc model is not strongly weighted ($w_i \leq 0.9$), I used a "full model averaging" approach testing all possible models (all-subset candidate set approach) using the "dredge" function in MuMIn package (Barton, 2012). From this I estimated an unbiased relative importance of the predictor variables for each species adding up the Akaike weights (w_i) for each model in which that variable appears (Burnham and Anderson, 2002; Symonds and Moussalli, 2011).

Table 2. Candidate models tested for seedling emergence and seedling survival. The models were the same for both response variables, and for all the species. Abbreviations for the predictors are: D = density, E = mammal exclosure, pH = pH, OrgSoil = organic soil, GroCov = ground cover, CanCov = canopy cover. Model 5 represent the null model with no fixed predictors.

Model number	Parameters included
1	D * E + (1|station)
2	D + E + (1|station)
3	D + (1|station)
4	E + (1|station)
5	~1 + (1|station)
6	D * E + pH + (1|station)
7	D * E + OrgSoil + (1|station)
8	D * E + GroCov + (1|station)
9	D * E + CanCov + (1|station)
10	D * E + pH + OrgSoil + (1|station)

4.4 Results

4.4.1 **Seed predation**

The effects of seed density and time on seed predation differed between species (Fig. 3). *Pseudopanax arboreus* (final survival = 89.1% at high density, and 88.9% at low density) and *C. robusta* suffered little predation (97.2% and 90.0%, respectively). *Dacrycarpus dacrydioides*, *P. ferruginea* and *B. tawa* were more predated, and density effects more evident for the two largest-seeded species. Seed density effects were present in the top models for *C. robusta*, *P. ferruginea* and *B. tawa*, however in *C. robusta* low seed densities had lower seed survival, opposite to what I found in *P. ferruginea* and *B. tawa* (Tables 3 and 4). None of the predictors were heavily weighted for *P. arboreus* or *D. dacrydioides* (Table 4). In the case of *P. arboreus*, I found almost no seed predation in this species; therefore it is expected not to find important effects of the predictors. Seed density was the main predictor for *B. tawa* seed predation, with a single model selected (Fig. 3, Table 3). The importance of seed density and reduction on survival at day 80 increased with seed volume (Fig. 4). Parameter estimates and details for the "best" model selected from the set of models tested are shown in Appendix 1.

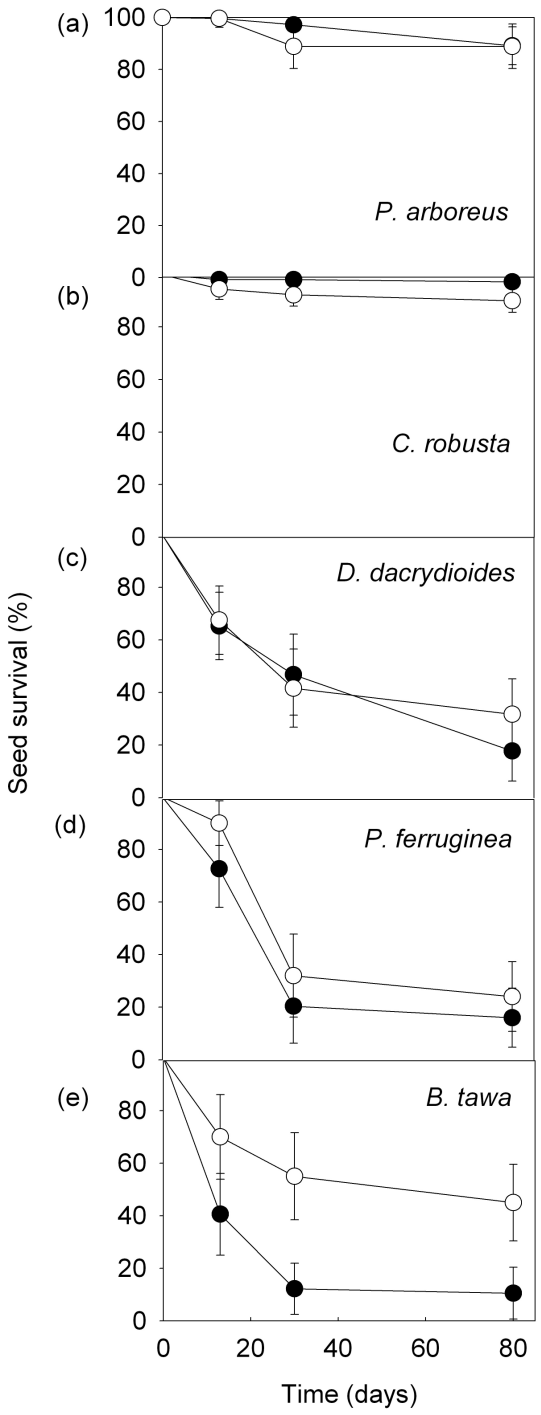


Figure 3. Seed predation represented as seed survival over time for *P. arboreus*, *C. robusta*, *D. dacrydioides*, *P. ferruginea* and *B. tawa* at high (filled circles) and low seed density (empty circles) in Blue Duck Scientific Reserve, Marlborough, New Zealand. Species are arranged from (a) to (e) in increasing seed size. Error bars represent ± 1 SE.

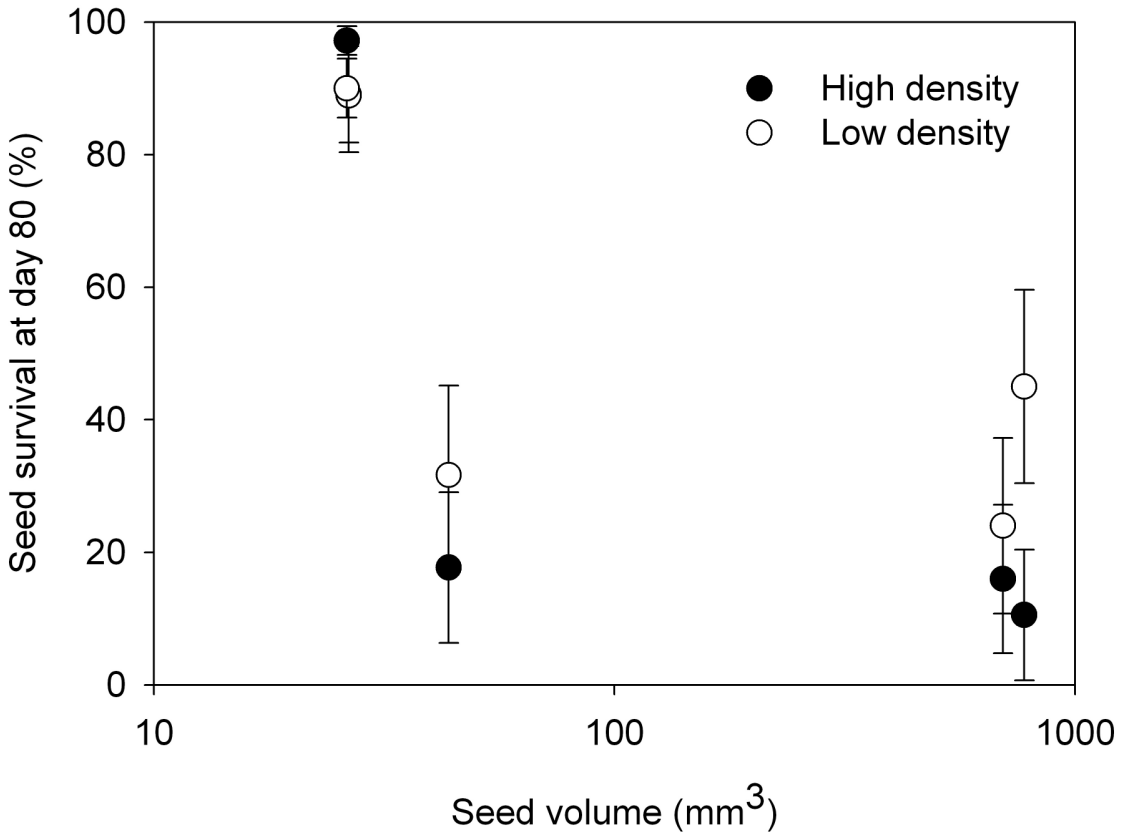


Figure 4. Seed survival at day 80 for five tree species as a function of seed volume (mm^3) at high (filled circles) and low (empty circles) seed densities. Note the log scale of the x axis.

Table 3. Selected top models for seed predation over time on *P. arboreus*, *C. robusta*, *D. dacrydioides*, *P. ferruginea* and *B. tawa*. Five generalized linear mixed effects models were formulated for each species and the best models, those having a cumulative Akaike weight (Cum. wi) ≥ 0.95, were selected. Model terms presented below show all fixed effects predictors only but random effects ((time|mesh) accounting for the experimental design and (1|ID) accounting for overdispersion when necessary) are included in all models.

Species	Model	K	log(ℒ)	AICc	Δ AICc	w_i	ER	Cum.w_i
P. arboreus	null	5	-52.7	116.5	0	0.46	1.00	0.46
	Time	6	-52.0	117.5	0.97	0.29	1.59	0.75
	Density	6	-52.7	118.9	2.41	0.14	3.29	0.89
	T + D	7	-51.9	120.0	3.48	0.08	5.75	0.97
C. robusta	T + D	7	-49.5	115.15	0	0.39	1.00	0.39
	Density	6	-50.87	115.33	0.18	0.36	1.08	0.75
	T * D	8	-49.44	117.71	2.56	0.11	3.55	0.86
	null	5	-53.53	118.16	3.01	0.09	4.33	0.95
D. dacrydioides	null	5	-107.45	226.01	0	0.6	1.00	0.60
	Time	6	-107.21	228	1.99	0.22	2.73	0.82
	Density	6	-107.4	228.39	2.38	0.18	3.33	1.00
P. ferruginea	Density	6	-70.12	153.83	0	0.65	1.00	0.65
	null	5	-71.99	155.08	1.25	0.35	1.86	1.00
B. tawa	Density	6	-72.36	158.3	0	0.99	0.66	0.99

Table 4. Cumulative Akaike weights (w_+) of predictors in seed predation models for species *P. arboreus*, *C. robusta*, *D. dacrydioides* and *P. ferruginea* in Blue Duck Reserve, Marlborough, New Zealand. For *B. tawa* no model uncertainty was found, as seed density was the only factor with support, therefore, model averaging is not necessary in this species. $\hat{\beta}$ represents the parameter estimate in the models. Cumulative weights can vary between 0 (no relative importance) and 1 (high relative importance). Tree species are ordered from smallest (left) to largest (right) fruit size. Density (L) represents the level "low" for the categorical predictor density. Values of $w+ > 0.5$ are presented in bold font.

	Plant species							
	P. arboreus		*C. robusta*		*D. dacrydioides*		*P. ferruginea*	
Predictors	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$
Density (L)	0.25	Negative	**0.85**	**Negative**	0.18	Positive	**0.65**	**Positive**
Time	0.40	Negative	**0.56**	**Negative**	0.22	Negative	0.00	
D(L) * T	0.03	Positive	0.11	Positive	0.00		0.00	

4.4.2 Seedling emergence and survival

The correlation tests between covariates show that pH and altitude were significantly correlated ($\rho = 0.88$, $t = 53.70$, $P < 0.001$), I therefore used only pH in the analysis as it has more biological sense.

As expected, I found neither constant effects of seed density nor exclusion of mammals on seedling emergence of the four species studied. Abiotic covariates were important only for *P. arboreus* and *C. robusta* (Tables 5,6 and 7), the species with the lower seed predation levels (Fig. 3). Germination was higher in *P. arboreus* at low seed densities (Fig. 5a), and the effects of exclosure treatment were stronger at this density too. However, its effects were accompanied by the effects of pH and organic soil, according to the top models selected. The calculation of the relative importance of biotic and abiotic predictors show that seed density and pH are strong predictors of *P. arboreus* germination, as well as a weaker effect of mammal exclosure (Table 7). In the case of *C. robusta* germination I found no clear effects of seed density or mammal exclosure (Fig. 5b). The top model selected in the analysis was the one with random effects only, followed by density and exclosure effects alone (Table 5). However, the relative importance of the predictors showed that pH and the amount of organic soil had the largest effects (across all possible models) on *C. robusta* germination, not seed density or mammal exclosure (Table 7). Seedling emergence in *D. dacrydioides* and *B. tawa* was strongly affected by mammal exclosure, but the

effects occurred in opposite directions (Tables 5 and 7, Figs. 4c and 4d). Germination in *B. tawa* increased in the open tubes, possibly due to increased attack from *C. querula* to seeds inside of the cages compared to seeds in open tubes, as well as possible seed desiccation. Parameter estimates and details for the "best" model selected from the set of models tested for seedling emergence are shown in Appendix 2.

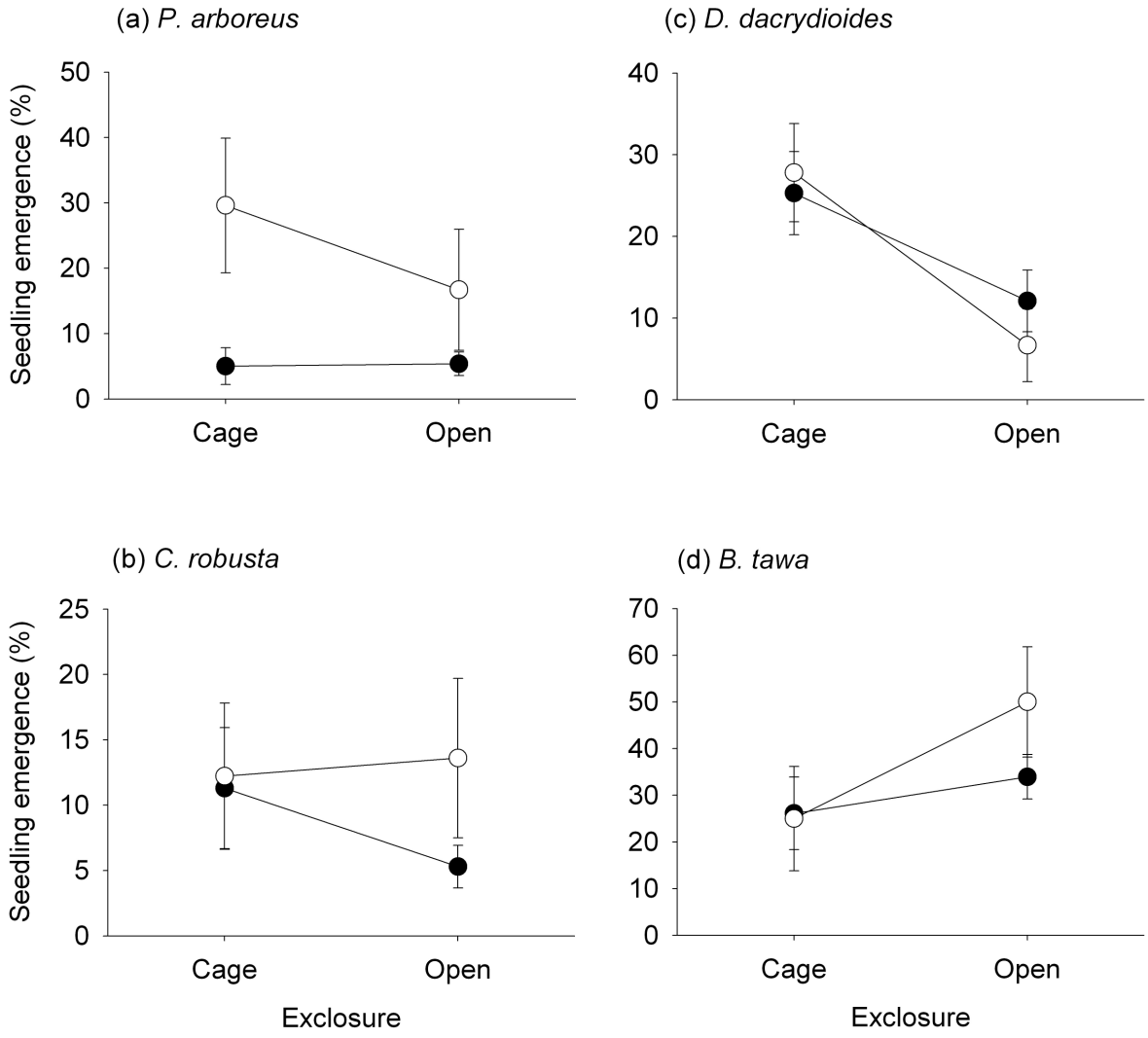


Figure 5. Effects of mammal exclusion on seedling emergence (mean ± SEM) for (a) *P. arboreus*, (b) *C. robusta*, (c) *D. dacrydioides* and (d) *B. tawa* at: high (filled circles) and low (empty circles) densities.

Table 5. Selected top models for seedling emergence of *P. arboreus*, *C. robusta*, *D. dacrydioides* and *B. tawa*. Ten *a priori* generalized linear mixed effects models were formulated for each species and the best models, those having a cumulative Akaike weight (Cum. wi) ≥ 0.95, were selected. Model terms presented below show all fixed effects predictors only but random effects ((1|station) accounting for the experimental design and (1|ID) accounting for overdispersion when necessary) are included in all models. Abbreviations for the predictors are: D = density, E = mammal exclosure, pH = pH, OrgSoil = organic soil, GroCov = Ground cover.

Species	Model	K	log($\mathcal{L}$)	AICc	Δ AICc	w_i	ER	Cum.w_i
P. arboreus	D * E + pH + OrgSoil	8	-36.0	93.3	0.00	0.74	1.00	0.74
	D * E + pH	7	-39.5	96.8	3.51	0.13	5.78	0.86
	D * E + OrgSoil	7	-39.9	97.8	4.51	0.08	9.52	0.94
	D	4	-45.3	99.8	6.52	0.03	26.04	0.97
C. robusta	null	3	-50.5	107.7	0.00	0.40	1.00	0.40
	D	4	-50.0	109.1	1.48	0.19	2.09	0.59
	E	4	-50.2	109.5	1.83	0.16	2.49	0.75
	D + E	5	-49.6	111.1	3.41	0.07	5.51	0.83
	D * E + pH	7	-47.0	111.6	3.98	0.05	7.32	0.88
	D * E + pH + OrgSoil	8	-45.5	111.8	4.14	0.05	7.91	0.93
	D * E + OrgSoil	7	-47.8	113.2	5.50	0.03	15.64	0.96
D. dacrydioides	E	4	-56.8	122.8	0.00	0.59	1.00	0.59
	D + E	5	-56.6	125.0	2.23	0.19	3.05	0.79
	D * E	6	-55.8	126.3	3.50	0.10	5.76	0.89
	D * E + CanCov	7	-55.6	128.9	6.10	0.03	21.14	0.92
	D * E + OrgSoil	7	-55.7	129.1	6.29	0.03	23.30	0.94
	D * E + GroCov	7	-55.8	129.2	6.41	0.02	24.66	0.97
B. tawa	E	4	-43.9	96.9	0.00	0.42	1.00	0.42
	null	3	-45.7	98.1	1.24	0.23	1.86	0.64
	D + E	5	-43.6	99.1	2.19	0.14	2.98	0.78
	D	4	-45.5	100.1	3.24	0.08	5.05	0.87
	D * E	6	-43.2	100.9	4.05	0.06	7.57	0.92
	D * E + GroCov	7	-42.2	102.1	5.19	0.03	13.37	0.95

Seedling survival was affected in all cases by the mammal exclosures, with most of the species having a reduced survival in the open units (Fig. 6, Table 7). The effects of the other predictors varied between species, again with abiotic predictors showing a higher relative importance for *P. arboreus* and *C. robusta*, compared to the other species. I found no important effects of seed density on *P. arboreus* (Fig. 6a) or *C. robusta* (Fig. 6b), but pH, organic soil and canopy cover were important factors for *P. arboreus* seedling survival, as well as the amount of ground cover for *C. robusta* (Tables 6 and 7). Seedling survival in *D. dacrydioides* was reduced in the open units, but only at high densities (Fig. 6c). Density was present in the top models selected for this species (Table 6) however mammal exclosure was clearly most important in the cumulative Akaike weights (Table 7). Opposite to what I expected, seedling survival for *B. tawa* was higher at high densities and in the open units (Fig. 6d). This might also be related to the attack of *C. querula*, as on several occasions I observed parasitized germinated seedling death inside of the cages. Seed density was the main predictor related to seedling survival in this species (Tables 6 and 7). Parameter estimates and details for the "best" model selected from the set of models tested for seedling survival are shown in Appendix 3.

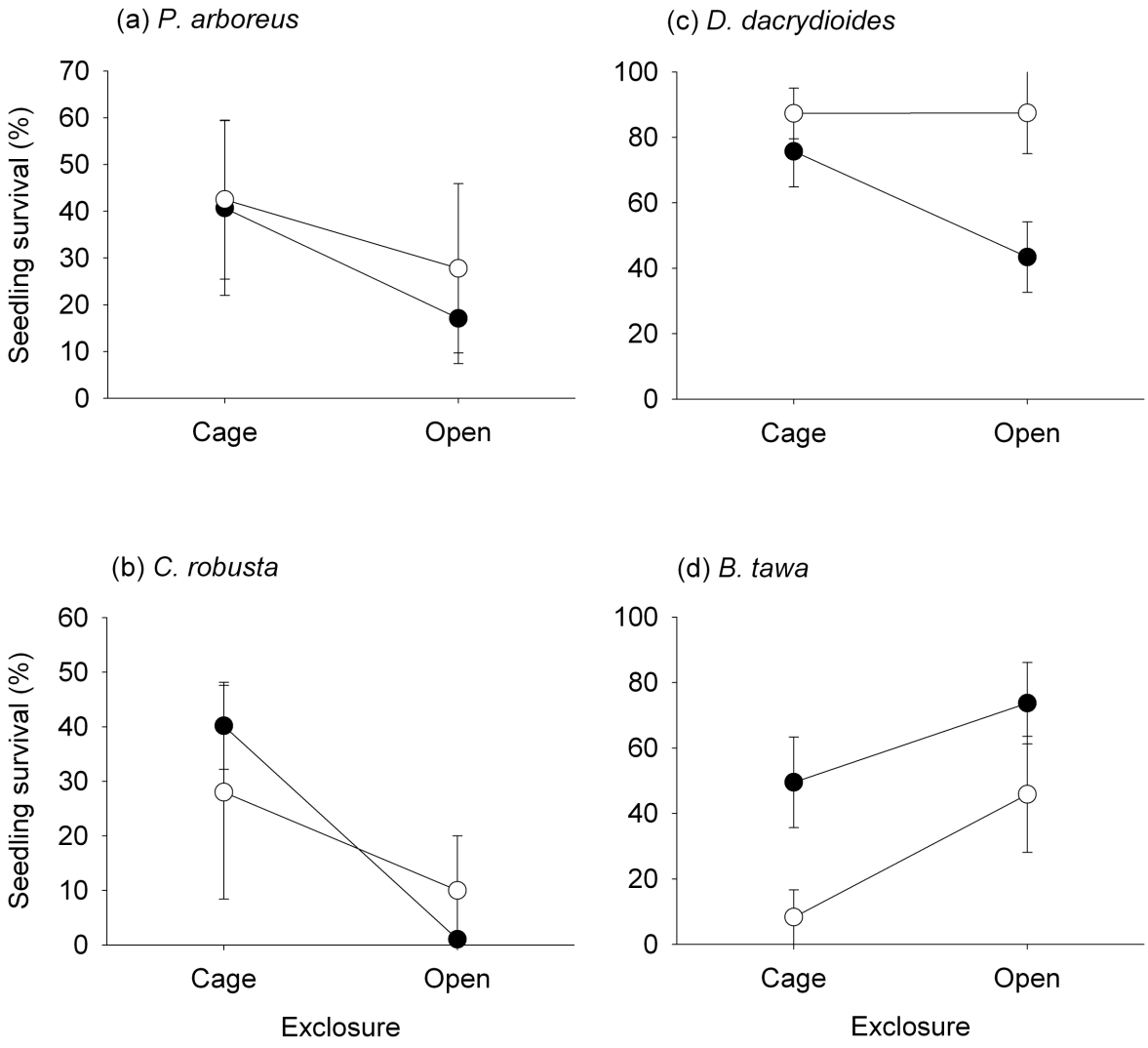


Figure 6. Effects of mammal exclusion on seedling survival (mean ± 1SEM) for (a) *P. arboreus*, (b) *C. robusta*, (c) *D. dacrydioides* and (d) *B. tawa* at: high (filled circles) and low (empty circles) densities.

Table 6. Selected top models for seedling survival of *P. arboreus*, *C. robusta*, *D. dacrydioides* and *B. tawa*. Ten *a priori* generalized linear mixed effects models were formulated for each species and the best models, those having a cumulative Akaike weight (Cum. wi) ≥ 0.95, were selected. Model terms presented below show all fixed effects predictors only but random effects ((1|station) accounting for the experimental design and (1|ID) accounting for overdispersion when necessary) are included in all models. Abbreviations for the predictors are: D = density, E = mammal exclosure, pH = pH, OrgSoil = organic soil, GroCov = Ground cover.

Species	Model	K	log(ℒ)	AICc	Δ AICc	w_i	ER	Cum.w_i
P. arboreus	D * E + pH + OrgSoil	7	-15.0	50.6	0.00	0.53	1.00	0.53
	D * E + pH	6	-17.7	51.8	1.15	0.30	1.78	0.83
	D * E + OrgSoil	6	-19.0	54.7	4.10	0.07	7.79	0.90
	D * E	5	-21.6	56.2	5.57	0.03	16.19	0.93
C. robusta	D * E + GroCov	6	-9.7	35.5	0.00	0.50	1.00	0.50
	D * E + CanCov	6	-10.2	36.7	1.14	0.28	1.77	0.78
	E	3	-15.8	38.6	3.02	0.11	4.53	0.88
	D + E	4	-15.2	40.2	4.63	0.05	10.13	0.93
	D * E	5	-13.8	40.4	4.88	0.04	11.47	0.98
D. dacrydioides	E	4	-35.2	80.0	0.00	0.39	1.00	0.39
	D + E	5	-34.5	81.6	1.56	0.18	2.18	0.57
	D * E + GroCov	7	-31.3	82.0	2.03	0.14	2.76	0.71
	D * E + CanCov	7	-31.5	82.4	2.43	0.12	3.37	0.82
	D * E	6	-33.8	83.5	3.49	0.07	5.72	0.89
	D	4	-37.2	84.1	4.07	0.05	7.63	0.94
	null	3	-39.1	85.2	5.18	0.03	13.32	0.97
B. tawa	D + E	5	-30.9	74.3	0.00	0.41	1.00	0.41
	D	4	-33.0	75.6	1.27	0.22	1.89	0.63
	D * E	6	-30.8	77.2	2.95	0.09	4.36	0.72
	null	3	-35.3	77.5	3.22	0.08	5.01	0.80
	E	4	-34.0	77.6	3.30	0.08	5.19	0.88
	D * E + pH	7	-29.9	78.9	4.63	0.04	10.14	0.92
	D * E + OrgSoil	7	-30.2	79.5	5.24	0.03	13.75	0.95

Table 7. Cumulative Akaike weights (w_+) of predictors in seedling emergence (emergence) and seedling survival (survival) models for species *B. tawa*, *D. dacrydioides*, *C. robusta* and *P. arboreus*. Seedling emergence and survival were followed for 12 months in Blue Duck Scientific Reserve, New Zealand. $\hat{\beta}$ represents the parameter estimate in the models. Cumulative weights can vary between 0 (no relative importance) and 1 (high relative importance). Values > 0.5 are presented in bold font. Tree species are ordered from smallest (left) to largest (right) seed size.

		Plant species															
		P. arboreus				*C. robusta*				*D. dacrydioides*				*B. tawa*			
		Emergence		Survival		Emergence		Survival		Emergence		Survival		Emergence		Survival	
	Predictors	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$	$w+$	sign of $\hat{\beta}$
Biotic	Density (L)	**0.99**	**Positive**	0.43	Negative	0.32	Positive	0.28	Negative	0.30	Negative	0.45	Positive	0.28	Positive	**0.74**	**Negative**
	Exclosure (O)	**0.56**	**Positive**	**0.91**	**Negative**	0.24	Negative	**1.00**	**Negative**	**0.99**	**Negative**	**0.91**	**Negative**	**0.55**	**Positive**	**0.57**	**Positive**
	D(L) * E(O)	0.46	Negative	0.19	Positive	0.02	Positive	0.13	Positive	0.09	Negative	0.18	Positive	0.04	+/-	0.08	Positive
Abiotic	pH	**0.92**	**Negative**	**0.94**	**Negative**	**0.70**	**Negative**	0.17	+/-	0.20	Negative	0.17	Positive	0.21	Negative	0.37	Negative
	Organic soil	0.36	Positive	**0.55**	**Negative**	**0.60**	**Positive**	0.17	+/-	0.22	Negative	0.19	Negative	0.22	+/-	0.33	Positive
	Ground cover	0.35	Positive	0.21	Positive	0.21	+/-	**0.86**	**Positive**	0.24	+/-	0.33	+/-	0.45	Positive	0.17	+/-
	Canopy cover	0.23	+/-	**0.60**	**Negative**	0.23	Negative	0.33	Positive	0.26	+/-	0.36	Positive	0.39	Negative	0.18	+/-

4.5 Discussion

In this study I focused on the effects of seed density and seed/seedling predation on the recruitment of five plant species in a New Zealand temperate forest. I also included abiotic variables as covariates for germination and seedling survival assessments. In general, the importance of seed density for seed predation increased with seed size, and the access or exclusion of vertebrate seed and seedling predators was the most important predictor for plant survival. Surprisingly, some species presented increased survival when seeds/seedlings were open to mammal access (germination *P. arboreus* and *B. tawa*, seedling survival *B. tawa*) but in general survival decreased when mammal access was permitted.

4.5.1 **Effects of density on seed predation**

As expected, seed predation increased with seed size, probably because of the greater seed attractiveness and nutritional contents (reward) in larger seeds. Previous research has reported contradictory results. A meta-analysis by Moles et al. (2003) found no significant relationship between seed size and seed predation after 24 hours the seeds were exposed. Larger seeds can suffer from increased mortality (Willson and Whelan, 1990; Hulme and Borelli, 1999), or reduced mortality (Alcántara et al., 2000), when compared to smaller seeds. A recent study using artificial seeds in a pine forest in southwestern China found that seed size was the most important factor influencing seed removal (predation and caching) by rodents (Wang and Chen, 2009). A factor frequently variable between studies on seed predation is the monitoring period. Seeds are exposed to seed predators until they are naturally buried (Hulme and Borelli, 1999) or start germination, therefore studies on this topic should consider following up seed survival for at least half of the time the seeds will be available to predators, when possible.

Seeds of *P. ferruginea* often disappeared from meshes, without leaving a trace of seed predation. The seed coat in this species is thick, and therefore would take some time to a predator to access to the nutritional tissue inside, so seeds may be removed for the animal to chew through the seed coat in a more sheltered location. This species also is one of the few tree species in NZ forests that can form a large, long-lived seed bank. Its seeds can survive up to 7 years in the field (D. Kelly and J. Ladley unpublished data). Seeds from this species and *Elaeocarpus dentatus* have been found accumulated in the trunks of the tree ferns in two other temperate forests in New Zealand (Sarah Richardson, pers. comm.). However, no *P. ferruginea* seedlings were found in standing tree fern trunks at Waitutu forest in the south of the South Island (Gaxiola et al., 2008). It is possible that seed removal of *P. ferruginea* seeds could be increasing its recruitment in concealed microhabitats, where the rats might carry the seeds for eating (Wilson et al., 2003), however research regarding the possible role of introduced mammals as secondary seed dispersers in New Zealand temperate forests is still lacking (but see O'Connor & Kelly in press).

Seed predation on the small seeded species was negligible; however time and density were important predictors in *C. robusta* survival. *Coprosma* reduced survival at low densities might be an artifact of the experiment, as seeds were long shaped and small, and difficult to glue to the meshes. It is possible that the probability of seeds becoming detached from the mesh was higher for this species (with no need of predators action) compared to the others.

The results from two previous studies in New Zealand analyzing the effect of seed size on seed removal rates are contradictory. In a podocarp-broadleaved forest in the center-east of the South Island Berry (2006) found a gradual but constant increase in seed predation by possums and rats with increasing seed size (as in this study), but the opposite trend for invertebrate attack. The results reported here present a higher rate of seed predation compared to a previous study by Moles & Drake (1999) on short-term post-dispersal seed predation on a secondary forest in Karori reserve in the Wellington area. Although their site was known to contain ship rats, Norway rats, house mice and brushtail possums, the minimum percentage of seeds cleaned from pulp (as the ones in my study) remaining at the end of the experiment (16 days) were 93.75% of *B. tawa* and 95% of *P. ferruginea*. They placed five seeds in depots of 10 x 10 cm (open ground and pot treatments combined), a density similar to my low density treatment. In my study seed survival at day 13 (low density) was 70% for *B. tawa* and 90% for *P. ferruginea*, a higher seed predation than they found. Some of the possible explanations to these differences are: (1) the densities of predators were lower in their study site, compared to the ones at mine (2) my experimental design (seeds glued to meshes) increased the conspicuousness of the seeds, and therefore the absolute levels of seed predation may be higher in my study than otherwise expected. Final seed survival in my study for *B. tawa* and *P. ferruginea* was 45% and 24% respectively, which reinforces the importance of extended monitoring times for seed predation in the field (80 days).

Seed density was an important predictor also for *B. tawa* and *P. ferruginea* seed predation, the largest seeded species in the experiment. Seeds in the high density treatment were proportionally more attacked than seeds at low density, probably due to the conspicuousness of the arrangement (Figs. 2d and 2f) and the nutritional reward for the consumption of these species (Janzen, 1971). In general, high seed densities increase the risk of seed predation, or the probability of encounter or the proportion of seeds predated (Willson and Whelan, 1990; Hulme and Borelli, 1999), however the increase in seed predation with seed density is not always stronger for larger-seeded species (Willson and Whelan, 1990). In a previous study in deciduous woodlands north-east of England Hulme and Borelli (1999) found that the increase in seed encounter at high seed density was a negative function of seed size, probably because large seeds were already being found at low densities, therefore the increase in seed density did not change significantly the proportion of large-seed seed depots found by the predators, that was already

high. In my study, survival from seed predation of medium and large-seeded species (*D. cupressinum*, *P. ferruginea* and *B. tawa*) at the end of the experiment was never higher than 45%, a high rate of seed predation compared to the 88% of survival in the worst case for the small-seeded species (*P. arboreus* and *C. robusta*). This trend in my data with seed size is consistent with these general principles, but I recognize that other ecological factors such as microhabitat characteristics and neighboring vegetation (among others) can alter the outcome in particular cases (Janzen, 1971; Willson and Whelan, 1990; Wilson et al., 2007).

All the vertebrate seed predators that forage at ground level in New Zealand forests are exotic mammals (Veblen and Stewart, 1982). Seeds of *P. ferruginea* are eaten by rats and less often by pigs (Beveridge, 1964; Campbell, 1978); possums eat the flesh but discard the seed unharmed (Williams et al., 2000). Seeds of *B. tawa* are eaten frequently by possums, and pigs, but not by rats or mice (Beveridge, 1964; Knowles and Beveridge, 1982). This study is the only one to evaluate seed predation on a group of tree species that are not necessarily masting species or large-seeded species only. More research on the effects of these seed predators on common species of New Zealand forests is needed, to understand the possible impact of these exotic species on current forest regeneration.

4.5.2 **Germination and survival**

Seed and seedling predation was the most important determinant of seedling emergence (exclosure $w+ > 0.5$ in three of the four species), and of seedling survival ($w+ > 0.5$ in all four species). Abiotic factors like pH and the depth of organic soil were strong predictors for seedling emergence, and seedling survival but only for the two small-seeded species *P. arboreus* and *C. robusta* which had lower predation levels. In this study the factors determining seed survival and germination in the small-seeded species were somewhat different to the factors determining seedling survival. However, for the medium and large-seeded species (*D. dacrydioides* and *B. tawa*) the factors determining these two stages of recruitment were, in general, the same.

I found that abiotic factors are more important for small-seeded species (in the range of my study) than for large seeded species, but in both ontogenetic stages. In a recent study Clark et al. (2012) found that abiotic factors were more important for seedling emergence than for seedling survival. The seeds studied by Clark et al. were all as small as or smaller than the smallest species in my study. It is possible that due to their small seed size their dependence on obtaining nutrients from the environment in the first few months is higher than that for larger-seeded species (Metcalfe and Grubb, 1997). The differences in the requirements of the small-seeded species in my study for seed germination and seedling recruitment could constitute opportunities for niche differentiation between the species (Grubb, 1977; Silvertown, 2004; Pérez-Ramos and Marañón, 2011; Clark et al., 2012).

The effects of mammalian predators on seed survival, germination and seedling survival were important across all the species. Rats and brushtail possums consume the small seedlings of several plant species in New Zealand forests (Campbell, 1978; Sweetapple, 2003; Wilson et al., 2003, 2006; Sweetapple et al., 2004; Grant-Hoffman and Barboza, 2010), and deer browsing impacts seedlings larger than 10 cm tall (Wilson et al., 2006). However the list for the species consumed as seedlings by brushtail possums and rats is not fully described yet. Most of the studies on possum diet are based on stomach contents, where is practically impossible to distinguish whether plant material comes from seedlings or adult leaves (Wilson et al., 2003). Although there are a number of anecdotal reports of herbivory by rats, more information from controlled experiments on the actual rates of seedling predation by rats are needed.

In general, survival increased when mammals were excluded, but surprisingly, in my study some species presented decreased survival when seeds/seedlings were inside mammal exclosures (germination for *P. arboreus*, germination and seedling survival for *B. tawa*). However, I suspect that the decrease in seedling survival could be a consequence of my study design preventing litter fall inside the cages. Even though some litter was added in the cages on top of seeds at the beginning of the experiment, and after each visit, it is possible that *B. tawa* seeds died from desiccation inside of the cages as they are very sensitive to drying out (Knowles & Beveridge 1982). Seed desiccation is however unlikely for *P. arboreus*, as this is an early successional species that recruits in gaps and open sites, and it is probably very tolerant to desiccation, and I do not have a possible explanation for this result.

Seed density was important for germination of *P. arboreus* (higher germination at low densities) and seedling survival of *B. tawa* (lower survival at low densities), and had weak effects on the other species across the two development stages. This result was unexpected for *P. arboreus*, as I found that seed density had no effect on seed predation rates for this species. In an experiment set up under controlled conditions at the University of Canterbury glasshouses I sowed the same numbers of *P. arboreus* seeds at the same densities as in the field, and during the same season seeds were sowed in the field. I found that *P. arboreus* seeds in high density germinated by yearly pulses, with 90% of the pots presenting new germination of between 3 and 20 seeds per pot 10 months after the beginning of the experiment. Final survival after 14 months did not differ between high and low seed densities (mean = 69.4% in high density, 80% low density, t-test $P = 0.097$). As germination is slower in the field compared to the glasshouse it is likely that ongoing germination of the original seeds occurred after the experiment was finished, therefore, seed density effects in germination of this species could only be detected during the first year. Clark et al. (2012) found that, across five randomly selected species, increasing the seed density increased seedling emergence up to 3 months, but decreased seedling survival to 24 months.

However, the results per species show that this pattern was important in only one of their five species, and that in general high densities slightly decreased survival up to three months but didn't have effects on seedling survival (Appendix E in Clark et al 2012). My results, together with results from previous studies (Willson and Whelan, 1990; Alcántara et al., 2000; Pérez-Ramos and Marañón, 2011) show that the effects of seed density on seedling emergence and survival are species-specific and highly variable, therefore generalizations across species can be misleading and are not recommendable.

4.5.3 **Concluding remarks**

My results coincide with those of Clark et al. (2012) in that biotic factors, specifically mammalian seed and seedling predators are the main determinants of seed survival and recruitment. In contrast to their study site, where the predator fauna was intact (Clark et al., 2012), the assemblage of ground vertebrate seed and seedling predators in New Zealand is composed entirely of exotic species. Rats, pigs, deer and brushtail possums (among others) predate on seeds and/or seedlings, reducing the recruitment of several plant species in New Zealand temperate forests (Beveridge, 1964; Beveridge and Daniel, 1965; Campbell, 1978; Veblen and Stewart, 1982; Wardle et al., 2001; Wilson et al., 2006). Most of these species have been present in New Zealand for less than 200 years, and the spread of some of them, like the brushtail possum to the top of the North Island and the south-west corner of the South Island, has been completed in only the last 15 years (Wilson, 2004; King, 2005). Due to the recent introduction of these species the long-term impacts of their feeding habits are still to be seen, and the evidence of the research published in New Zealand and overseas during the last years indicate that these effects could be present at several ecological levels (population, community, ecosystem) and on not only indigenous plant communities but also on soil animals and vertebrate groups (Suzuki et al. in press; Beveridge, 1964; Campbell, 1978; Bellingham and Allan, 2003; Wilson et al., 2003; Innes et al., 2004; Sweetapple et al., 2004; Spear and Chown, 2009; Grant-Hoffman and Barboza, 2010). Given the high levels of predation, and the wide variation among plant species in predation levels, there could be long-term shifts in species composition due to mammal predation which have yet to be reflected in current canopy composition. The long-term ecosystem impacts of invasions are however extremely difficult to forecast with certainty.

4.6 Appendix 1

Best model estimates and errors (in brackets) per species for seed predation on *P. arboreus*, *C. robusta*, *D. dacrydioides*, *P. ferruginea* and *B. tawa*. Best model was chosen as the one with the lowest number of parameters (K) whose ΔAICc < 2. The parameter Time and its interaction with Density were absent from the top model for all species.

Species	K	Intercept	Density	R^2_{LR}
P. arboreus	5	7.90 (1.09)		
C. robusta	6	7.14 (0.77)	-2.41 (1.09)	0.10
D. dacrydioides	5	3.27 (1.04)		
P. ferruginea	5	3.60 (1.26)		
B. tawa	6	-3.64 (1.11)	4.80 (1.21)	0.21

4.7 Appendix 2

Best model estimates and errors (in brackets) per species for seedling emergence on *P. arboreus*, *C. robusta*, *D. dacrydioides* and *B. tawa*. Best model was chosen as the one with the lowest number of parameters (K) whose ΔAICc < 2. Ground cover and Canopy cover were never retained in the best selected model. Abbreviations for the predictors are: D = density, E = mammal exclosure, pH = pH, OrgSoil = organic soil. R^2_{LR} = pseudo-R squared based on the likehood-ratio test.

Species	K	Intercept	D	E	D * E	pH	OrgSoil	R^2_{LR}
P. arboreus	8	10.27 (4.20)	2.68 (0.52)	0.95 (0.50)	-2.33 (0.84)	-2.42 (0.69)	0.03 (0.02)	0.61
C. robusta	3	-2.93 (0.32)						
D. dacrydioides	4	-1.35 (0.35)		-1.43 (0.38)				0.28
B. tawa	3	-0.88 (0.23)						

4.8 Appendix 3

Best model estimates and errors (between brackets) per species for seedling survival on *P. arboreus*, *C. robusta*, *D. dacrydioides* and *B. tawa*. Best model was chosen as the one with the lowest number of parameters (K) whose ΔAICc < 2. Parameters organic soil and canopy cover were never retained in the best model. Abbreviations for the predictors are: D = density, E = mammal exclosure, pH = pH, GroCov = Ground cover. R^2_{LR} = pseudo-R squared based on the likehood-ratio test.

Species	K	Intercept	D	E	D*E	pH	GroCov	R^2_{LR}
P. arboreus	6	20.86 (5.99)	-1.60 (0.67)	-2.56 (0.67)	1.74 (1.04)	3.41 (1.02)		0.78
C. robusta	6	-3.22 (0.71)	-0.43 (0.73)	-3.07 (1.04)	2.26 (1.48)		0.04 (0.01)	0.85
D. dacrydioides	4	2.09 (0.57)		-2.34 (0.68)				0.87
B. tawa	4	1.30 (0.78)	-3.02 (1.32)					0.80

CHAPTER 5

Beilschmiedia tawa (tawa) seedlings at high density

5 Janzen-Connell effects on two tree species in a temperate forest of New Zealand

5.1 Abstract

1. The Janzen-Connell hypothesis postulates that the highest probability for successful recruitment occurs at intermediate distances from the parent, due to higher mortality near the parent and a reduced probability for the seeds to reach large distances away from parent. Studies testing this hypothesis in temperate forests are scarce, and largely from the northern hemisphere.

2. Using a split-plot experimental design I measured the effects of (a) the presence of conspecific canopy, (b) high conspecific seed densities and (c) introduced (or invasive) mammal access on seedling emergence and seedling survival to 20 months for two canopy tree species of the New Zealand temperate forest, *Dacrycarpus dacrydioides* (Podocarpaceae) and *Beilschmiedia tawa* (Lauraceae). Seeds and seedlings of both species are attacked by mammals; however, *B. tawa* seeds are also attacked by the larvae of a host-specific moth, *Cryptaspasma querula*. I therefore expected to find stronger support for Janzen-Connell effects in *B. tawa* than in *D. dacrydioides*.

3. Recruitment of the two species was reduced under conspecific canopies (*D. dacrydioides* by 64%, *B. tawa* by 90%, compared to away from conspecific canopies). High seed density reduced *B. tawa* (but not *D. dacrydioides*) seedling emergence by 35% relative to low density, but increased seedling survival by 65%, relative to low density values. Mammalian predators reduced *B. tawa* (but not *D. dacrydioides*) seedling emergence by 72%. Seedling survival in *D. dacrydioides* (but not in *B. tawa*) was reduced by mammals by 86%.

4. Distance effects were stronger than density effects, and mediated by native and exotic predators. Final survival under conspecifics was strongly reduced in both species, with zero survival of *B. tawa* under conspecifics, and near zero (2/896) under *D. dacrydioides*. This is required for Janzen-Connell hypothesis to maintain diversity in forests, but is not usually found. These results, together with previous research in New Zealand forests give support to Janzen-Connell effects in New Zealand temperate forests.

5.2 Introduction

The Janzen-Connell hypothesis (Janzen 1970 and Connell 1971) was proposed to explain the high plant diversity present in tropical systems, and has stimulated much research in community ecology. In their hypothesis, Janzen and Connell postulate that the highest probability for successful recruitment occurs at intermediate distances from the parent, where the probability for a seed to be deposited and the probability of surviving are intermediate. The main causes of high propagule losses

near the parent are seed and seedling mortality due to host-specific biotic agents (pathogens, seed predators and seedling herbivores). Only if survival under the parent is zero will the effect of these agents generate negative density-dependent recruitment (starting at the parent tree with the highest seed density), stopping mono-specific stands developing, and increasing species diversity (Hubbell, 1980).

Several reviews have been done on testing the Janzen-Connell hypothesis (HilleRisLambers et al. 2002, Hyatt et al. 2003, Carson et al. 2008, Terborgh 2012 some of the most recent ones), with contrasting results. Seed predation rates and the proportion of species affected by density-dependent mortality were found not to be different between tropical and temperate ecosystems (HilleRisLambers et al., 2002; Moles and Westoby, 2003). Although Hyatt et al. (2003) found no significant effects of distance from the parents on overall propagule survival, their review must be interpreted with care as: (1) wasn't focused on studies explicitly addressing the Janzen-Connell hypothesis (see their search terms, page 592 Literature search) (2) did not include experiments where different types of seed/seedling predators were tested, or only pathogens or diseases, main elements in the Janzen-Connell hypothesis, (3) did not considered experiments on natural seed fall or naturally occurring seedlings , (4) was biased towards seed predation experiments (129/152 data points) with few studies in seedling survival. Their abstract states "we... conclude that further testing to explore this hypothesis as a diversity-maintaining mechanism is unnecessary", a statement with broad implications based on a narrow spectrum of studies. Carson et al. (2008) on the contrary, focused their review on studies explicitly testing Janzen-Connell hypothesis with no restriction on journals or types of predators. Their results are based on percentages of studies carried out in the different ecosystem types and particular sites. They also focus a large part of the review on areas (geographical and of knowledge) where more research is needed, and general caveats of the studies. Overall, they found that distance and/or density effects are recurrent across studies, common in the tropics but under-evaluated in the temperate ecosystems. Terborgh (2012) acknowledges the difficulty of finding significant results across such a diversity of monitoring extensions, experimental designs and ontogenetic stages. He focuses his review largely (but not exclusively) on the results of extensive studies he and his group have obtained in Cocha Cashu Biological Station in the Amazonian, through different ontological stages of plants. When density and distance effects are isolated, distance effects are more common than density effects (Terborgh, 2012). He points out that bi-trophic interactions (interactions between seed/seedling predators and the plants) are the main mechanism for Janzen-Connell effects, and that propagule density influences the attack rates by these agents, instead of generating density-dependent mortality through intra-specific interactions.

The distinction between density- and distance-responsive agents is important to evaluate the presence of Janzen-Connell effects (Janzen, 1971; Terborgh, 2012). Density-responsive agents are supposed to be distributed evenly in the environment, and to attack high propagule densities, independent of the distance from the source. Distance-responsive agents are unevenly distributed in

the environment, and their attacks are concentrated under the canopy of parent trees. Density-responsive agents are generally host-generalists vertebrate seed predators and herbivores. Distance-responsive agents are expected to be host-restricted, above ground or underground organisms smaller than 2 mm size (Janzen, 1970; Swamy and Terborgh, 2010; Terborgh, 2012).

However, for animal dispersed plants, high densities of seeds do not necessarily occur only under the parent canopy, but can also be generated by the disperser's feeding and resting behaviour (Howe, 1989; Kwit et al., 2004; García et al., 2007). Therefore, effects of high propagule density away from parental canopies are also likely to be detrimental for the species recruitment due to the presence of density-responsive agents. There is, however, less research in this area. Janzen-Connell studies often fail to distinguish between density and distance effects (Carson et al., 2008; Terborgh, 2012). Full factorial experiments are necessary to disentangle the effects of density and distance, as well as experiments including the exclusion of different guilds (different sized seed predators, seedling herbivores; Terborgh 2012). A study by Packer and Clay (2000) in a temperate deciduous forest in Indiana (USA), and more recent studies in tropical and temperate forests have reported the results for complete factorial experiments on density- and/or distance-dependence effects of biotic agents on plant recruitment (Hautier et al. 2010, Swamy and Terborgh 2010, Wotton and Kelly 2011, among others). All of these studies have reported reduced seed and seedling survival under parental canopies, and stronger distance than density effects on survival. However, this type of study is still uncommon, and concentrated in tropical forests (Terborgh, 2012).

Tests of the Janzen-Connell hypothesis are scarce in temperate forests. In the review by Carson et al. (2008) on 53 articles published between 1970 and 2006, 85% of the studies occurred in tropical forests, and only 15% (eight studies) in temperate forests. Those eight studies from temperate forests were concentrated in the Northern hemisphere, and seven of them on deciduous temperate forests. Those few studies, together with more recent temperate zone recent ones (Wilson et al. 2007, Yamazaki et al. 2009, Martin and Canham 2010, Wotton and Kelly 2011), show evidence of density- and distance-dependent effects on temperate tree species (Hyatt et al., 2003; Carson et al., 2008), and even similar sized effects for seed predation and density-dependent mortality in temperate and tropical forests (HilleRisLambers et al., 2002; Moles and Westoby, 2003). However, there is still a lack of research in this topic, where Wilson et al. (2007) and Wotton and Kelly (2011) are, to my knowledge, the only published studies testing Janzen-Connell effects in temperate forests of the southern hemisphere.

The aim of this chapter was to measure the effects of density-responsive and distance-responsive biotic agents, on seed survival, germination and recruitment of one small (*Dacrycarpus dacrydioides*, Podocarpaceae) and one large-seeded tree species (*Beilschmiedia tawa*, Lauraceae) in a temperate rainforest in New Zealand. Using a complete factorial experimental design I tested for seedling emergence and seedling survival to 20 months of these two species under three factors: distance from conspecifics (under/away), seed density (high/low) and predator access (cage/open) to

the seeds and seedlings. Chapter 4 showed that seed predation rates were higher for larger seeded species at the site, and the presence of a host-specific invertebrate seed predator has been previously described in the large-seeded species *B. tawa* (Beveridge, 1964) but not for the small-seeded species *D. dacrydioides*. I therefore expect to find: (1) No effects of distance from conspecifics on *D. dacrydioides* survival, due to the attack by generalist predators, but increased *B. tawa* mortality under conspecifics, due to attack by host-specific agents (2) No seed density effects on *D. dacrydioides* (as no effects were found in Chapter 4) but strong seed density effects on *B. tawa* recruitment (as found in Chapter 4) (3) Exclusion of mammalian predators will increase recruitment for both species, and this effect will be stronger away from conspecific canopies and at high densities, as seed/seedling predators will track high densities of resources.

5.3 Methods

5.3.1 **Study site and species**

The research was carried out in Blue Duck Scientific Reserve (42°14' S, 173°47' E, 400 m elevation), Marlborough district, South Island of New Zealand. This Reserve contains a rare example of mature mixed podocarp forest (Norton and Courtney, 2000). The climate is oceanic cool-temperate characterized by warm summers and mild winters, with a summer (January) average minimum temperature of 6.6° C, and maximum of 28.8° C, and in winter (July) minimum temperature of 2.5° C and maximum of 18.8° C (New Zealand Meteorological Service, 2012). Annual rainfall is moderate with 1400-1600 mm (Breese et al. 1986). Soil pH ranges between 6.9 and 7.2 in the upper 150 mm of soil; this, together with other soil characteristics, is expected to produce moderate to high fertility for the plants (Hurst et al., 2002).

The dominant canopy species in the reserve are emergent *Dacrydium cupressinum*, *Prumnopitys taxifolia* and *Podocarpus totara* (all Podocarpaceae). Also present are *Dacrycarpus dacrydioides* and less abundant *Prumnopitys ferruginea*, but both of them sparser than the other podocarps. The canopy layer formed by these species reaches 22 m. A lower angiosperm canopy (12-15 m) is also present with *Melycitus ramiflorus* (Violaceae), *Elaeocarpus dentatus* (Elaeocarpaceae), *Hedycarya arborea* (Monimiaceae) and *Alectryon excelsus* (Sapindaceae). Several small patches of *Beilschmiedia tawa* (Lauraceae), are scattered through the Reserve, where *B. tawa* is locally dominant in the angiosperm canopy (Norton and Courtney, 2000).

Beilschmiedia tawa and *D. dacrydioides* were selected as study species, due to their large differences in fruit sizes (*B. tawa* fruit: 15.5 mm wide, *D. dacrydioides*: 5.11 mm, Fig. 1a), their differences in seed predator assemblages and fast germination from fresh seeds. Blue Duck is almost the southern distribution limit of *B. tawa* (Knowles and Beveridge, 1982). This has the fourth largest fruit in New Zealand (Kelly et al., 2010). The fruit of *B. tawa* is dark purple, 15.5 mm wide and up to

30 mm long (Allan, 1961; Kelly et al., 2010). The New Zealand pigeon (*Hemiphaga novaeseelandiae*, kereru) is the main disperser of *B. tawa*, mainly because with a body weight of ca. 650 g it is one of the few species that can consume the large fruits (Kelly et al., 2010). The population of NZ pigeons has declined since human arrival in New Zealand; however, today its populations are increasing due to predator control and reductions in illegal hunting (Innes et al., 2010). Tui (*Prosthemadera novaeseelandiae*: Meliphagidae) also disperse *B. tawa* seeds, but are less abundant than the NZ pigeon in the study site.

Dacrydium dacrydioides presents a small-arilated round seed (fruit hereafter, Fig. 1a). The average total fruit length (n=100 fruits) is 10.1 mm, seed width 4.4 mm and aril width 5.1 mm. It presents highly variable fruiting across years (Beveridge, 1973), and can be described as a masting species. Seven bird species have been described as seed dispersers for *D. dacrydioides*, all of them present in the study area (for a detailed description of the seed dispersers see Table 1 in Chapter 3).

Hand-cleaned seeds from *B. tawa* germinate within a few months of ripening in the field, usually in high proportions (mean = 70%, seven records, Kelly et al. 2010). Germination of hand-cleaned seeds of *D. dacrydioides* under controlled conditions in the shade house averages 92% and takes about 4 months to start (Burrows, 2001). Limited information is available for germination of bird-dispersed seeds of *B. tawa* in the field (24%, one record, in Kelly et al. 2010) or *D. dacrydioides*.

5.3.2 **Experimental design**

In this study I focused on the germination and survival of bird-dispersed seeds. Seeds from *B. tawa* and *D. dacrydioides* were scarce in the study site the year the experiment was started; therefore, seeds from two different sites were used. Bird-dispersed *B. tawa* seeds (clean seeds) were collected from Pelorus Bridge Scenic Reserve (41°18'S - 173°35'E) in Marlborough district, 106 km north-west of Blue Duck. Bird-dispersed seeds of *D. dacrydioides* (with no aril attached) were collected from Riccarton Bush in Christchurch (173 km south-west from the study site). From both species the seeds were collected from at least 10 different adult trees in the forest, and mixed prior to the experiment. The New Zealand pigeon is capable of making long-distance flights and their home-ranges can range between 619 and 31 732 ha (Powlesland et al., 2011) and is also able to move through human-induced fragmented habitat (Innes et al., 2010).

(a)

(b)

Figure 1. (a) Fruits of *Beilschmiedia tawa* (left) and *Dacrycarpus dacrydioides* (right) (b) Cages for the mammal exclosure treatment. Seeds in *D. dacrydioides* sits on top of the fleshy aril (orange). Both species possess single-seeded fruits.

I used a split-plot design to compare seed predation, seedling emergence and survival of *B. tawa* and *D. dacrydioides* in Blue Duck SR, following the experimental design by Wotton and Kelly (2011) but without the "undispersed-fruit" (whole fruit) treatment due to a shortage in fruit availability. I tested three treatments, each with two levels: (i) distance: under a conspecific versus 20 m away (ii) mammal exclusion: caged versus open (iii) seed density low versus high (for *B. tawa* 4 versus 18 seeds in a 120 mm diameter circle, for *D. dacrydioides* 12 versus 100 seeds). Seed numbers for density treatment were based in previous experiments on similar species (Wotton and Kelly, 2011) and long-term seed rain collections in the site (Kelly D. and Ladley J.J. unpublished data). Each conspecific tree had all treatments (factorial combinations of seed density and mammal exclusion) below its canopy, and was paired spatially with a location 20 m away. Canopies of *B. tawa* rarely extend more than 8m beyond the main trunk (S. Richardson pers. comm.), and 20 m. was the maximum possible distance reachable from an adult of one of the two species, without getting closer to a conspecific. *Beilschmiedia tawa* has a patchy distribution in the Reserve, I therefore selected trees from the edge of the largest *B. tawa* patch identified inside Blue Duck, and moved away from the edge for the locations away from conspecifics. *D. dacrydioides* trees were scattered inside and around the *B. tawa* patch. Locations away from *D. dacrydioides* trees were selected based on the distance from conspecifics and absence of canopy from other Podocarpaceae species that might interfere with seed germination of closely related species. All the locations (under and away) selected had similar canopy cover (75% - 100%) and thus light levels.

Seeds were prevented from rolling away and being lost by placing them inside open-topped and open-bottomed polycarbonate tubes 30 mm high and 120 mm diameter. Tubes were fixed to the ground using two wire pegs. To exclude vertebrate seed and seedling predators I constructed cages made of welded galvanized mesh with 5 mm aperture, 20 cm diameter and 30 cm high (Fig. 1b). For each species four tubes were placed in a square of one m side, under the canopy of each of eight conspecifics (i.e. n = 8), and a paired away location for each tree. The four factorial treatment combinations (low density/open, low density/caged, high density/open, high density/caged) were randomly assigned to tubes. Leaf litter was placed in the tubes on top of the seeds to minimize increased attraction to seeds coming from augmented conspicuousness. Tubes were monitored for 20 months; I recorded seed predation events, seedling emergence and seedling survival for each group of seeds or seedlings. In this study I will only consider seedling emergence and seedling survival for both species, as these two stages could be equally recorded. From now on, seedling emergence refers to seeds that survived seed predation and germinated, and therefore, "seedling emergence" include also the effects of seed predation. I analyzed separately the effects of seed predation on *B. tawa*, as I was able to count the number of eaten and parasitized seeds for this species, but not for *D. dacrydioides* due to its small seed size. Seeds were sowed in May 2010, but germination only started (roots emerging from seeds in the case of *B. tawa*) in December 2010 for *B. tawa*, and January 2011 for *D. dacrydioides* (seeds starting to be lifted from ground by the shoot). Tubes were checked every

six weeks for 5 months from the beginning of germination, and then one year after the beginning of germination, in January 2012 (seedlings one year old). At each visit litter from beside the cage was placed into the tubes, to emulate the natural litterfall on seeds the "open" treatment.

Causes of seed mortality in *B. tawa* and *D. dacrydioides* seeds and seedlings are diverse. Seeds from *B. tawa* suffer intense attack and mortality by the larvae of the moth *Cryptaspasma querula* in the North Island (Beveridge, 1964), however, some seeds can still germinate after being attacked, usually dying before forming the leaves. Exotic mammals also consume the seeds of these two species. In Blue Duck there is no pest (exotic mammal) control management in place, so I expect this site to hold high densities of predators. Mammalian seed and seedling predators present at Blue Duck are the exotic house mouse (*Mus musculus*), ship rat (*Rattus rattus*), the Norway rat (*R. norvegicus*), and brushtail possum (*Trichosurus vulpecula)* (King, 2005). Red deer *Cervus elaphus* also consume seedlings and young shoots of trees. Native invertebrate herbivores are also present. There is no evidence of seed caching by mammals in New Zealand (Wilson et al., 2007), however it is possible that for some species whose seeds remain viable in the soil for several years (e.g. *P. ferruginea*) seed removal could promote regeneration in hidden places where ship rats might take the seeds for safer consumption (Wilson et al., 2003). However neither *B. tawa* nor *D. dacrydioides* form seed banks, and in my experiment evidence of seed predation (empty seed coats and husks) was always found when seed numbers were reduced in the tubes.

5.3.3 **Statistical analysis**

I analyzed the effects of distance (near versus away), mammal exclusion (open versus caged) and density (high versus low) on seedling emergence and seedling survival separately, per species (four full models). I also analyzed the effects of distance and density on overall seed predation (insects + mammals) on *B. tawa*. To disentangle the particular effects of insects or mammals on seed predation I used the seeds in the open treatment as an estimator for mammal seed predation, and the seeds inside cages to estimate insect seed predation. Generalized linear mixed models allow the use of non-normal error distributions and hierarchical random effects. As the response variables were always proportions (predated seeds, germinated seeds or seedlings surviving) I used a binomial error distribution with logit link for all models. To specify the experimental design in the models I included a random effects factor representing the nestedness of density and mammal exclusion within distance (subplot) within tree (1 to 8). I tested for overdispersion using the residuals of the model. If the model was overdispersed (overdispersion > 1) I added an extra random effect accounting for the observation-level variation (Bates et al., 2011). I used stepwise (backwards) model selection so the specific variables affecting seeds or seedling survival could be identified, and compared to a previous study on similar species and experimental design carried out in New Zealand (Wotton and Kelly 2011). This method has been criticized for several reasons (e.g. Whittingham et al. 2006) however in cases of

small amounts of model reductions it can still be considered appropriate (Pinheiro and Bates 2000, Bolker et al 2009). For all the analyses I used the "glmer" function included in the lme4 package (Bates et al., 2011) in R software version 2.14.1 (R Development Core Team, 2011). Figures represent seed germination and seedling survival proportions calculated from data with their 95% confidence intervals (CI).

5.4 Results

Location under conspecifics significantly reduced seedling emergence and survival in both species (Table 1). High seed density and access to mammals were also detrimental, but not in all cases. I found no significant interaction between factors for *B. tawa* seedling emergence or survival.

Seedling emergence of *D. dacrydioides* and *B. tawa* were reduced under conspecific adults by 57% and 49% respectively, compared to the away treatment (*D. dacrydoides*, from 20.0% to 8.4 %; *B. tawa* from 33.5 % to 17.2 %; Fig. 2). I found no significant effects of exclosure or density on *D. dacrydioides* seedling emergence. The access of vertebrate seed predators reduced *B. tawa* seedling emergence from 41.0% to 11.5%, as well as high seed densities reduced emergence from 30.8% to 19.6%.

Table 1: Results from Generalized Linear Mixed effects models for seedling emergence and survival. Final significant factors retained in the minimum model were selected using backwards selection procedure. The level of each factor is indicated in the table for an easier interpretation of the estimates. Only factors retained in the last model are shown. Interaction between exclosure and density, and three way interaction were never retained in the final (minimum) model. * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

			Emergence		Seedling Survival	
Species	Parameter	Level	estimate ± SE	P	estimate ± SE	P
D. dacrydioides						
	Intercept		-1.90 ± 0.37	***	0.89 ± 0.67	
	Location	under	-1.52 ± 0.52	**	-1.44 ± 1.04	
	Exclosure	open		ns	-2.63 ± 0.46	***
	Density	low		ns	-0.62 ± 0.49	
	Location*Exclosure	under:open		ns	-4.82 ± 1.97	*
	Location*Density	under:low		ns	4.96 ± 1.59	**
	df		6		9	
B. tawa						
	Intercept		-0.26 ± 0.43		0.41 ± 0.42	
	Location	under	-1.33 ± 0.55	*	-2.50 ± 0.81	**
	Exclosure	open	-2.69 ± 0.56	***		ns
	Density	low	0.82 ± 0.29	**	-2.07 ± 0.60	***
	df		7		6	

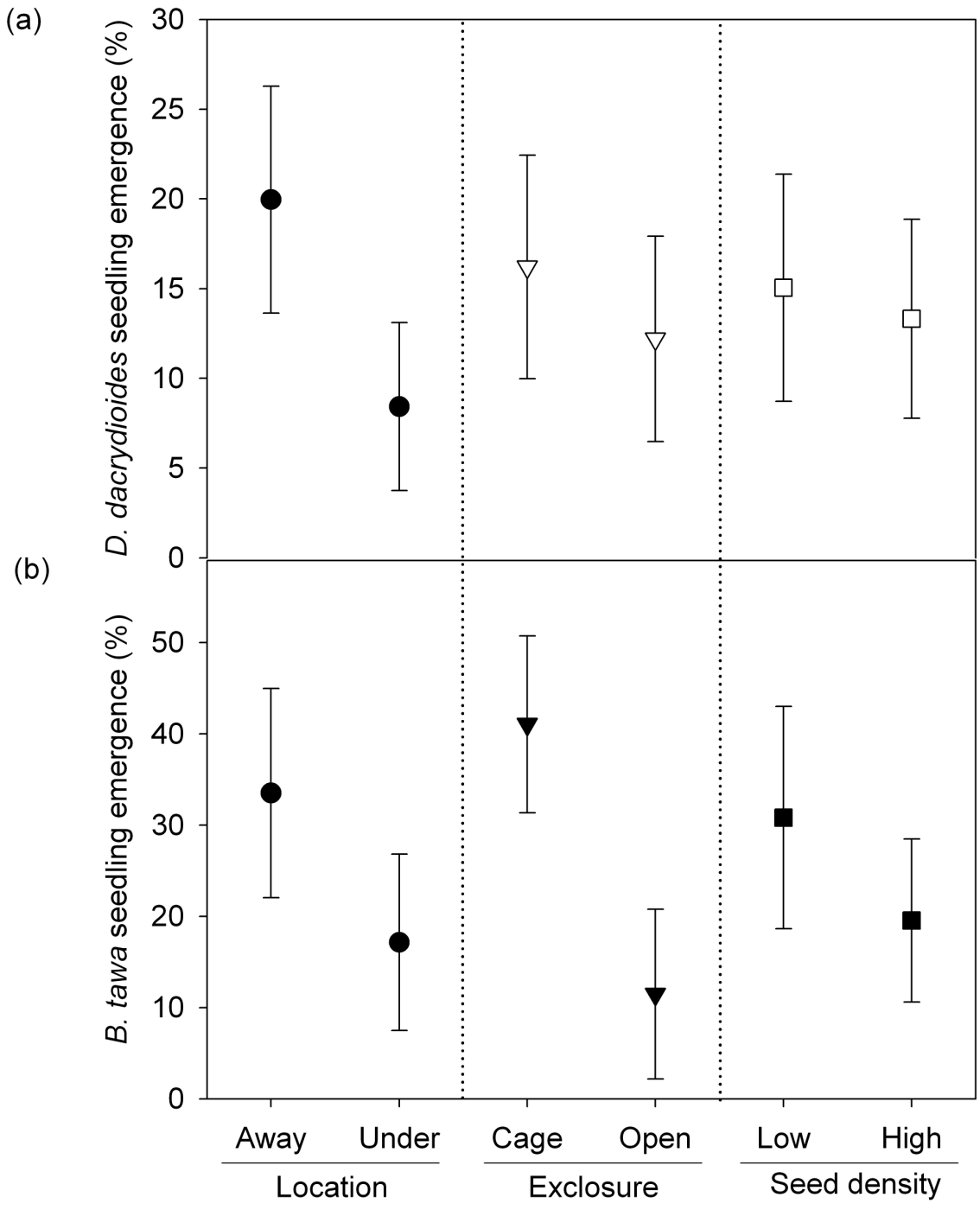


Figure 2. Percentage of seedling emergence for *D. dacrydioides* (a) and *B. tawa* (b), in response to the main effects of the predictors (location, exclosure and seed density). Total number for *D. dacrydioides* tubes is n = 62 (31 in each level) and for *B. tawa* n = 57 (from left to right 29, 28; 27, 30; 30, 27). Filled symbols represent significant effects ($P < 0.05$).

Seedling survival of the two species was affected differently by the different factors (Figs. 3a and 3b). In *D. dacrydioides* open access to seedling predators reduced seedling survival by 86.3% (Fig. 3a), from 62.1% of germinated seeds surviving as seedlings to only 8.5%. The effect of location for *D. dacrydioides* seedling survival was dependent on the level of the other two treatments (significant interactions between location and exclosure, and between location and density, Table 1). High densities increased seedling survival away from conspecifics, but reduced it under conspecifics compared to low density (Fig. 4a). On the other hand, the reduction of seedling survival by herbivores was less variable under conspecifics than away, and larger compared to cages (Fig. 4b). Location and seed density were the main factors affecting *B. tawa* seedling survival (Fig. 3b). The percentage of surviving seedlings of *B. tawa* away from conspecifics was 41.2%, in contrast to only 6.19% under conspecifics (85% reduction). Seedlings of *B. tawa* in high density showed a higher survival (41.6%) than seedlings in low density (14.6%), as in *D. dacrydioides*, this effect tends to be larger for seedlings away from conspecifics (non-significant interaction effect due to high variability between replicates, Appendix 1).

Overall seed predation on *B. tawa* did not differ between distances, seed densities or exclosure treatments (Table 2). Only eight of 330 seeds in the open treatment were found as insect predated, I therefore used the open treatment as a proxy for mammal seed predation, and the cages as a proxy for insect seed predation. Seed predation by mammals in the open exclosure treatment in *B. tawa* was not significantly affected by location (mean $_{under}$ = 71.18 ± 23.03% seeds predated, mean $_{away}$ = 58.93 ± 27.51%), density (mean $_{high}$ = 65.93 ± 26.74% seeds predated, mean $_{low}$ = 65.00 ± 23.86%) or the interaction between them (Table 3). However, seed predation by insects inside cages was higher under *B. tawa* conspecifics, with 84.0% (± 13.1 CI) of the seeds attacked under conspecifics, but 54.8% (± 20.5 CI) attacked away. Seed density and the interaction between density and location were not retained in the final model for insect predation inside of cages (Table 3).

In summary, the effects of distance from conspecific canopy on recruitment were present across all ontogenetic stages (seed predation, seedling emergence, and seedling survival) in both species, but the effects of seed density depended on the ontogenetic stage and the species. Overall, seeds away from con-specifics, protected from mammal attack and at low densities presented the highest seedling emergence and survival in both species (Fig. 5a). Seeds unprotected, in high densities and under conspecific trees presented lowest seedling emergence and survival. Seedling emergence for *D. dacrydioides* in the first scenario was 27.4%, and 16.7% of initial seeds were alive as seedlings after 20 months; contrasting with only 7% in the second and zero alive after 20 months (Fig. 5a). The contrast was even larger for *B. tawa* seedling emergence, 47% of the seeds presented seedling emergence in the away/cage/low density scenario and 12.5% after 20 months, but only 0.7% in the under/open/high density one and zero alive after 20 months. The effects of distance from conspecifics for *B. tawa* were larger than for *D. dacrydioides*, with final survival being reduced from 14.1 to 1.36% for *B. tawa*, and 8.15 to 1.95% in *D. dacrydioides* (Fig. 5b).

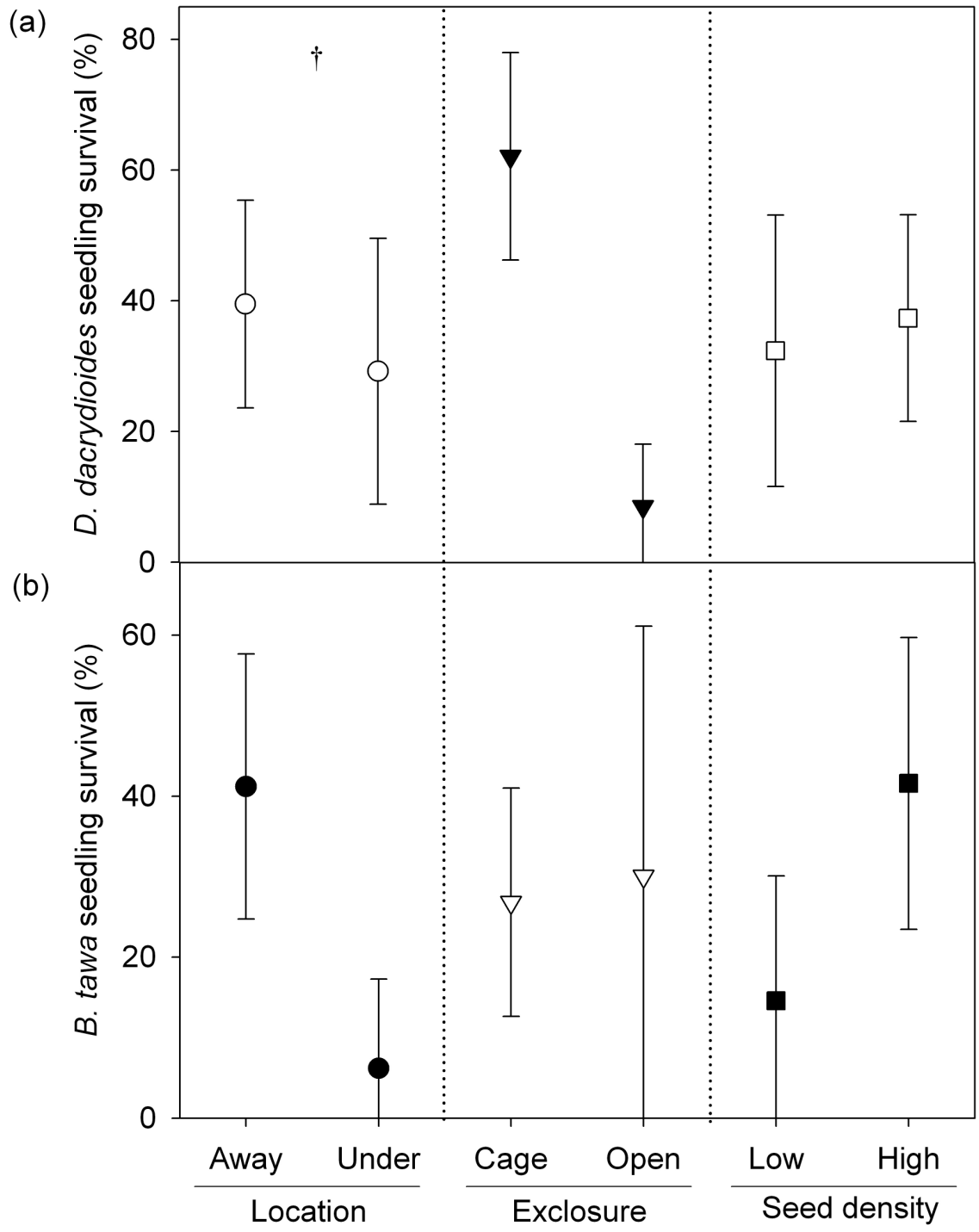


Figure 3. Percentage of seedling survival for *D. dacrydioides* (a) and *B. tawa,* in response to the main effects of the predictors (location, exclosure and seed density). Only tubes with seed germination > 0 were considered in the seedling survival analysis. Total number for *D. dacrydioides* tubes is n = 44 (from left to right: 26, 18; 22, 22; 18, 26) and for *B. tawa* n = 31 (19, 12; 23, 8; 16, 15). Filled symbols represent significant effects; † = significant through its interaction with exclosure and with seed density, see Fig. 4.

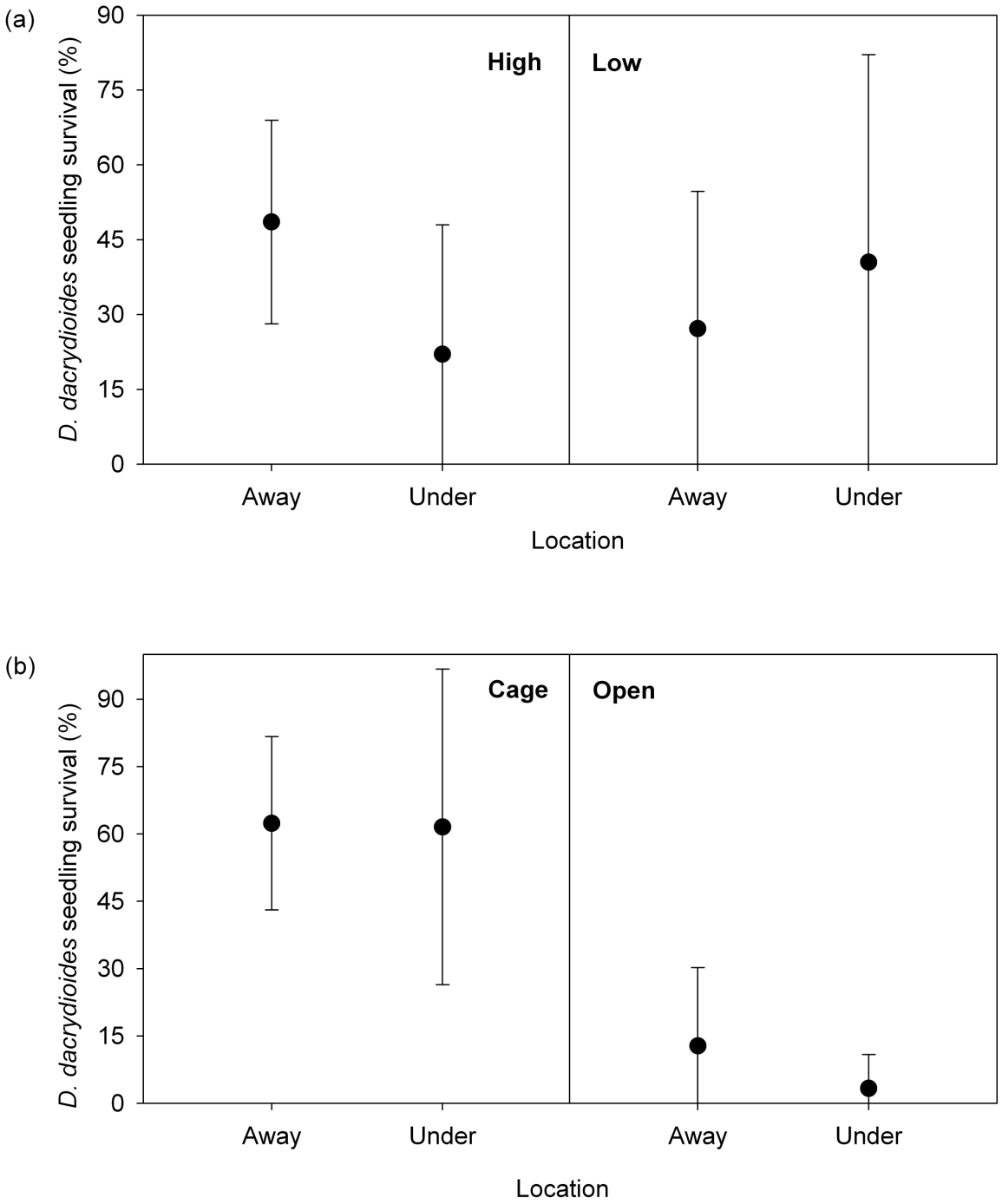


Figure 4. Interactions between location and density on *D. dacrydioides* seedling survival at: (a) high density (left panel) and low density (right panel), and (b) mammals excluded (cage, left panel) and mammals not excluded (open, right panel). Total tube numbers from left to right: (a) 15, 11, 11, 7 and (b) 14, 8, 12, 10.

Table 2: Results from Generalized linear mixed effects models for overall seed predation on *B. tawa* seeds. The level of each factor is indicated in the table for an easier interpretation of the estimates. All factors are shown as none of them was significant.

Parameter	Level	estimate ± SE	P
Intercept		0.76±1.14	
Location	under	1.51±1.55	ns
Exclosure	open	0.65±1.57	ns
Density	low	-0.54±0.47	ns
Location * Exclosure	under:open	0.17±2.31	ns
Location * Density	under:low	1.00±0.97	ns
Exclosure * Density	open:low	0.47±0.95	ns
Location * Exclosure * Density	under:open:low	-0.60±1.95	ns
df		11	

Table 3: Results from Generalized linear mixed effect models for seed predation by insects and mammals on *B. tawa* seeds. For insect predation analysis was ran using only seeds in cages, and for mammal predation seeds in open. Level of each factor is indicated in the table for an easier interpretation of the estimates. Only factors retained in the last model are shown for insect predation. All factors are shown for mammal predation as none of them was significant. * = P < 0.05

		Insect predation		Mammal predation	
Parameter	Level	estimate ± SE	P	estimate ± SE	P
Intercept		0.47 ± 0.55		1.51 ± 2.53	ns
Location	under	1.88 ± 0.87	*	1.12 ± 3.22	ns
Density	low		ns	1.04 ± 1.10	ns
Location * Density	under:low		ns	-2.52 ± 1.51	ns
df		4		6	

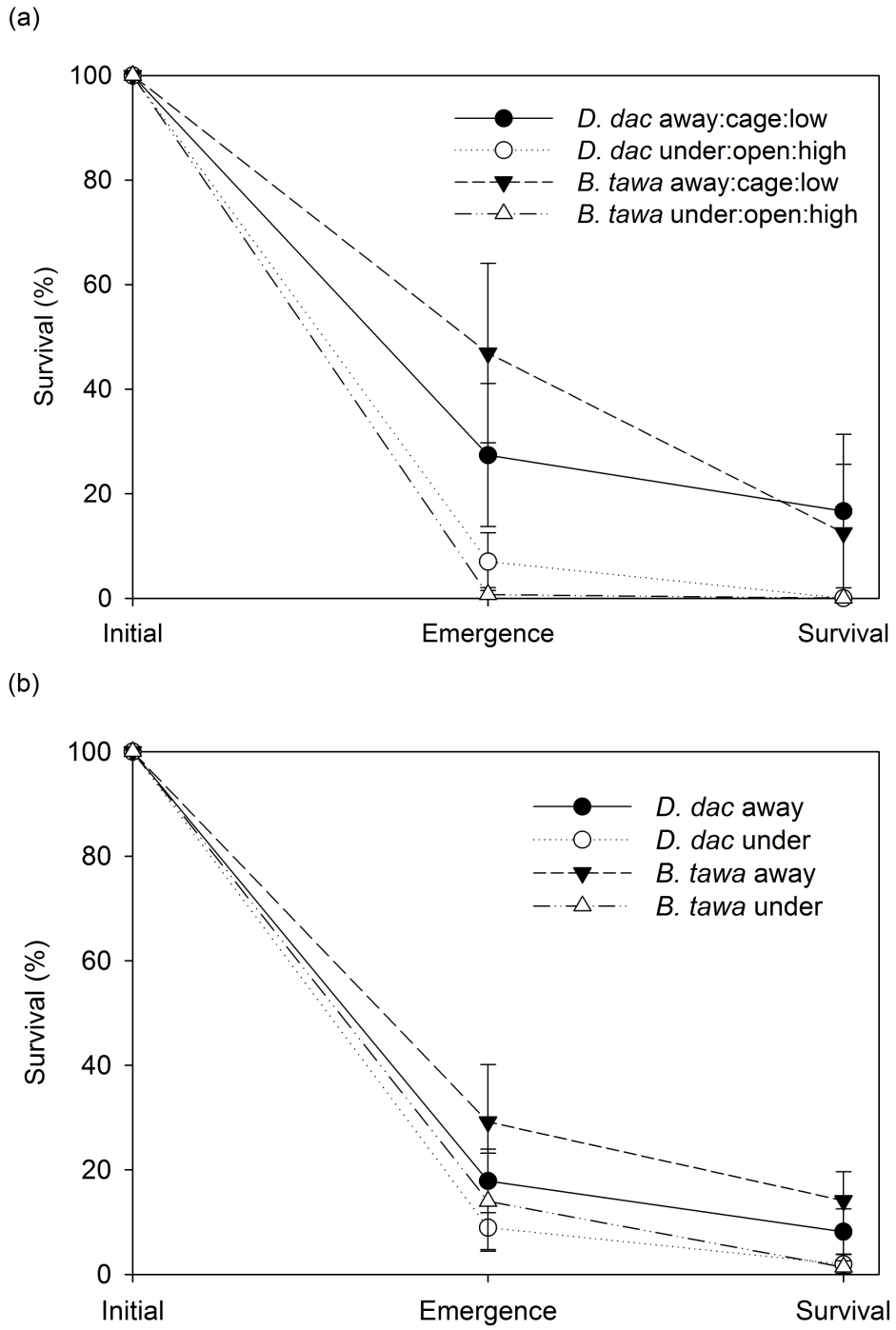


Figure 5. Mean remaining survival for *D. dacrydioides* and *B. tawa* during 20 months from sowing the seeds where (a) cumulative survival in the two most extreme survival scenarios for both species, (b) main effects of distance from conspecifics on cumulative survival. Seeds were placed at different locations (under versus away from conspecifics), different seed densities (high = 100 seeds in *D. dacrydioides* and 12 in *B. tawa*; low = 12 in *D. dacrydioides* and 4 in *B. tawa*) and with different access to predators (cage = mammalian predators excluded, open = mammalian predators not excluded). Emergence records reflect the effects of seed predation and seed germination together.

5.5 Discussion

In my study, the effects of location were present not only in *B. tawa* as expected (Hypothesis 1), but also in *D. dacrydioides*, through seedling emergence and seedling survival, showing reduced survival under conspecifics for both species. Seed density, as expected (Hypothesis 2) was important for *B. tawa* but not for *D. dacrydioides*. Seedling emergence and seedling survival of *B. tawa* were affected by seed density; however, the effects occurred in opposite directions, with higher survival under low density during emergence, but increased seedling survival at high seedling densities, coincident with the results found in Chapter 4. The effects of excluding large seed/seedling predators were important for both species as expected (Hypothesis 3). Seedling emergence of *B. tawa* increased when mammalian predators were excluded, as well as *D. dacrydioides* seedling survival. The diversity of the effects framed in the Janzen-Connell hypothesis on the two species I studied here show that: (1) Janzen-Connell effects can be detected in temperate evergreen forests (2) distance-effects are the most important factors early in the recruitment process (3) seed density and exclusion of seed/seedling predators are species-specific and vary with ontogeny.

5.5.1 **Janzen-Connell effects on seedling emergence**

The percentage of seeds that escaped predation and germinated successfully (seedling emergence) was reduced under conspecifics. The reduction of seedling emergence is explained mainly through increased seed predation under conspecifics, either by host-specific agents (*C. querula* in *B. tawa*) or introduced mammals (house mouse, rats, brushtail possums). I did not find evidence of seed mortality or reduced germination due to soil pathogens as it was not in the aims of this study; however this is not evidence for its absence. The moth *C. querula* attacks *B. tawa* seeds on the forest floor, and the larvae develop inside the seed, consuming the endosperm and the embryo. Attacks of the host-specific predator to *B. tawa* seeds were higher under conspecifics than away; however mammal attack to seeds was not different under or away from conspecifics. These results agree with what was postulated by Janzen (1970) forty years ago, and supported by others more recently (Swamy and Terborgh, 2010; Alvarez-Loayza and Terborgh, 2011). Janzen proposed that distance-responsive predators are more likely to be parasites associated to the adult trees, therefore not highly mobile, in contrast to density-responsive predators, like mammals, that will be attracted from the surroundings by high densities of propagules. In my study, even the high seed density treatment was offered at a scale maybe too local for brushtail possums (19 seeds), I also found higher survival and germination of seeds in low seed densities, compared to high densities (independent of the location), confirming that mammalian seed predators in *B. tawa* are acting as density-responsive agents. Brushtail possums and pigs consume *B. tawa* seeds (Knowles and Beveridge, 1982). Possums are consumers of *B. tawa* fruits in the canopy, and expected to consume the seeds once the pulp has rotten on the ground (Beveridge, 1964; Knowles and Beveridge, 1982), especially in areas where vegetation cover has been reduced by deer

(Beveridge, 1964). Most of seed predation recorded on *B. tawa* seeds in Moles and Drake (1999) and in my previous chapter (Chapter 4) was also attributable to brushtail possums. The seeds of *B. tawa* have been described as "unpalatable" to the exotic rodents introduced in New Zealand (Knowles and Beveridge, 1982), however, there is some evidence of Pacific rats (*R. exulans*, absent from Blue Duck) eating *B. tawa* seeds in the forest (Stead, 1937) and ship rats eating fruits of *B. tawa* in the forest as well as in feeding trials (Innes, 1979), both are, however, incidental records. My results show that in *B.tawa* the synergistic effects of the native host-specific seed predator, together with the effects of the exotic mammals, reduce drastically recruitment under conspecific trees. *Beilschmiedia tawa* adults in this forest are patchily distributed (probably because of heterogeneity in soil quality for the species) but due to the recentness of the introduction of the exotic predators to New Zealand (introduced from 1840 onwards, Atkinson and Cameron 1993) it is possible that the joint effects of these seed predator groups together are not visible yet, and that more spaced recruitment of *B. tawa* will be visible at this site on a longer time-span.

Mammalian predators can sometimes act as distance-responsive agents when, for example, they use the adult trees as indicators of high densities of food in the form of seeds or seedlings (Janzen, 1971). Janzen named rodents as one possible group that could behave as a distance-responsive agent maybe because of their small body size, and this is precisely the group that act as seed predators for *D. dacrydioides* (Beveridge, 1964; Campbell, 1978), which also showed higher seedling emergence away from conspecifics. Seeds of *D. dacrydioides* are eaten by the kiore, the ship rat (Beveridge, 1964; Campbell, 1978) and probably house mouse (predator of *Dacrydium cupressinum* seeds, a similar fruited tree from the same family, Ruscoe et al. 2004). Hautier et al. (2010) found evidence for this pattern, as small but not large mammals in a Bornean forest behave as distance-responsive agents for seed predation of five dipterocarp species. Therefore, for density-responsive predators, their foraging behaviour can generate Janzen-Connell recruitment patterns, depending on their capacity to find signals for high densities of resources, like parental trees (Mari et al., 2008). *Dacrycarpus dacrydioides* has a highly variable fruit crop among years (Beveridge, 1964; Webb and Kelly, 1993). This fruiting pattern could explain the use of the adult trees as a food indicators by the seed predators. The low fruit production during the year I set the experiment constituted an extra advantage for the interpretation of the results. Because I had to use seeds from source sites different from the experimental site, background densities under conspecifics were relatively low. Masting behaviour has been postulated to increase the survival probability of the seeds through predator satiation (Kelly and Sork, 2002). Therefore, I would expect Janzen-Connell effects on masting species to be present in low fruiting years (as the one in this study), reducing the recruitment of conspecifics under the canopy, but absent in high years due to predator satiation.

A possible caveat of this study, as with all studies on seed predation where seeds are not tagged and followed, is the presence of mammal caching. Seed caching has not been formally described for New Zealand forests but rodents do move seeds before eating them (Wilson et al. 2003;

S. Richardson, pers. comm.). However, in the case seed caching happens in New Zealand forests, *B. tawa* seeds do not persist in seed banks, quickly losing its viability due to desiccation (Knowles and Beveridge, 1982). *Dacrycarpus dacrydioides* seeds reduce their germination, from 100% to 40% after 11 months of storage (Burrows, 2001) but some seeds can survive even after 2 years in the field (Enright and Cameron, 1988). Even so, in all instances of reduced numbers of seeds I found empty cases or husks as evidence of seed predation, for this I am certain of that my results represent actual seed loses due to seed predation.

5.5.2 **Janzen-Connell effects on seedling survival**

Seedling survival was reduced under conspecific canopies in both species. The higher survival of *D. dacrydioides* seedlings away from the canopy in high densities, but almost equal in low density confirms the results on seed survival and germination, and suggests that the agents predating seeds could be the same as the ones predating the seedlings (density-responsive agents behaving as distance-responsive). In an experiment in Mokoia Island (Rotorua Lakes, North Island, NZ) Norway rats ate the seedlings of podocarps, including *D. dacrydioides* together with *B. tawa* seedlings (Beveridge and Daniel, 1965). The rats reduced the number of podocarp seedlings by 20% during the winter of 1963. However, I also found damage to seedlings in two cages that cannot be attributed to rats. I found most seedlings in these two high density cages with the top nipped off (Fig. 6), under and away from conspecifics (both for tree number 1). This must have been an animal smaller than the 5 mm cage mesh, presumably an invertebrate such a slug or snail. I also found high *D. dacrydioides* seedling mortality with no explicit cause, as seedlings in the tubes were found entire but dead in several occasions. This was probably attributable to the presence of species specific pathogens; although I acknowledge the importance of these agents as the frequent responsible of distance - dependent patterns the identification of soil pathogens on the seedlings was beyond the scope of this study. Future experiments on seedling herbivory on this species should include setting video cameras to record the attacks in the field site, include exclosures able to exclude large invertebrates like Lepidopterans and molluscs, or use selective chemicals (molluscicide, fungicide) to determine the factors causing mortality (Terborgh, 2012).

Seedling survival of *B. tawa* was increased away from the parents, and surprisingly, also in high densities. These results seem contradictory to each other in the framework of Janzen-Connell hypothesis. However, it is possible that different seedling predators affect in different manners seedling survival, as it happened with seedling emergence in this species. The seedlings of *B. tawa* are consumed by Norway rats, possums and deer. Seedling herbivory on *B. tawa* by Norway rats has been recorded in Mokoia Island (Beveridge and Daniel, 1965), therefore this predator might be responsible for higher seedling mortality under conspecifics. The leaves have been described as of low palatability for possums where *B. tawa* is abundant (central North Island) but of increased palatability in the southern extreme of its distribution (e.g. Blue Duck Scientific Reserve; Knowles and Beveridge

1982). When deer densities are high *B. tawa* seedlings are heavily browsed, as well as new coppice shoots from stumps, however, is not a preferred food of this species (Knowles and Beveridge, 1982). Deer are commonly seen and heard in the Reserve and the site is favoured by local hunters during the hunting season because deer are known to be present at moderate densities. It is possible that due to the low seedling palatability for deer and possums, high densities of *B. tawa* seedlings allowed for higher proportions of seedlings to escape from herbivory (i.e. predator satiation) away from conspecifics.

Figure 6. Seedlings from *Dacrycarpus dacrydioides* with the top nipped off, attacked by invertebrates (caged high density treatment).

My study support previous research showing that rats and possums can have strong effects on seeds and seedlings in the forest. In a study in a mixed beech-podocarp-broadleaved forest with high rat abundances (ship rat and/or norway rat) and low numbers of possums, and in a broadleaf-podocarp forest with low numbers of rats and high numbers of possums, the most abundant species (rats or brushtail possums) was responsible for significant reductions in seedling survival (Wilson et al., 2003). Their results show that at high rat or possum densities the reduction in seedling survival can be drastic, and that at high possum densities, possum impacts can double rat impact.

5.5.3 **Janzen-Connell effects in temperate forests**

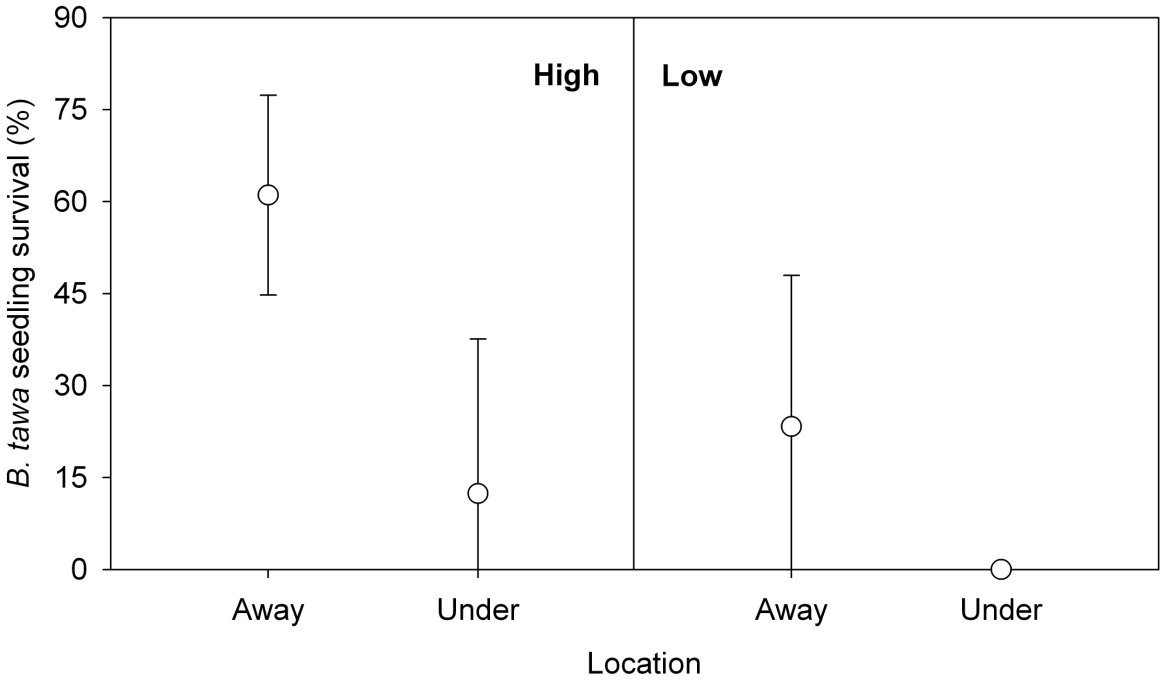
When Janzen (1970) and Connell (1971) created what we now call the Janzen-Connell hypothesis, their aim was to explain the possible mechanisms behind the high plant diversity in tropical forests. Janzen (1970) remarks "I believe a third generalization is possible about tropical tree species as contrasted with temperate ones: for most species of lowland tropical species, adults do not produce new adults in their immediate vicinity (where most seeds fall)". However, along the text, he stresses the possibility of distance- and/or density-dependent effects in tropical and temperate forests when there is low tree density, high species richness and regular spacing between the adults. A review by Carson et al. (2008) including research done in temperate forests explicitly testing Janzen-Connell effects published between 1970 and 2006, together with a search for papers published between 2006 and 2012 show that most of the studies (19/21) were done in temperate deciduous forests in the northern hemisphere, and only two studies in southern hemisphere temperate rainforests, both in New Zealand, where most tree species are evergreen. Results from the studies in temperate forests in the northern hemisphere are mixed, however with high frequency of negative density- or positive distance-dependent effects (Carson et al., 2008). Of the two studies in New Zealand temperate forests, one studied neighbourhood effects on seed predation by rodents in a mixed conifer-angiosperm forest in the South of the South Island (Wilson et al., 2007). The second studied the effects of dispersal failure in two large seeded species in lowland forest sites in northern North Island (Wotton and Kelly, 2011). Wilson et al. (2007) results show that seeds from *Nothofagus solandri* var. *cliffortioides* (Nothofagaceae) and *Dacrycarpus cupressinum* (Podocarpaceae, a conifer) were more likely to escape from predation if placed > 15 m from parents of both taxa, as both species are masting species with an abundant predator in common, the house mouse. *Beilschmiedia taraire* (Lauraceae) and *Corynocarpus laevigatus* (Corynocarpaceae, both large-fruited angiosperms) on the other hand presented significant reductions of between 20-30% in their survival under conspecifics two years after sowing (Wotton and Kelly, 2011), similar to my results for *B. tawa* here. The present evidence therefore for New Zealand temperate forests (plus the effects of native host-specific predators as *C. querula* and the potential non-evaluated effects of soil pathogens) suggest that Janzen-Connell effects are present, and that could be contributing to the maintenance of diversity in these temperate forests.

New Zealand forests are a particular case, where all the mammalian seed and seedling predators did not evolve with the native plants, as they were introduced by Maori 800 years ago (kiore) and Europeans in successive introductions since 1840 (Atkinson and Cameron, 1993). The presence of Janzen-Connell effects for *D. dacrydioides* through the actions of these introduced species could indicate that, independent from local interactions between animals and plants that evolved in the same site, these animals could have large impacts on diversity in many of the multiple ecosystems where they have been introduced (Ruscoe et al., 2004; Wilson et al., 2007; Grant-Hoffman and Barboza, 2010). Future research in temperate ecosystems should (1) intend to emulate more appropriate high density situations for the targeted seed/seedling predators, e.g. increase seed density

at a tree scale, more than a cm. scale, as generalist seed predators might be searching for high density spots as seeds under parent trees; and (2) aim for longer-term studies to determine if recruitment to advanced sapling stages is possible near the parent or conspecifics.

5.6 Appendix 1

Location effects on *B. tawa* seedling survival at: high (left panel) and low (right panel) seed densities. Seedling survival at low density under conspecifics was zero in all tubes. Total tubes numbers from left to right are 9, 6, 10 and 6.



CHAPTER 6

Peg chewed by deer

6 Synthesis

The spatial aspects of animal-mediated seed dispersal have received more attention in the last 10 years (Nathan and Muller-Landau, 2000; Schupp et al., 2010), stimulated, among others, by the development of new complex tools to analyze these patterns (Levey and Sargent, 2000; Godoy and Jordano, 2001; Perry and Dixon, 2002; Carlo et al., 2007; Wiegand et al., 2009). The consequences of the presence or absence of seed dispersal on seed survival, germination and recruitment are dependent on multiple factors: abiotic (litter, soil moisture, light) as much as biotic (pathogens, seed predators, biotic), specially for animal dispersed species. During recruitment, plant propagules (seeds, seedlings) go through these filters, determining what individuals will replace the pre-existing ones (Grubb, 1977). In New Zealand the current condition of the avifauna (the main seed dispersers in pre-human times, Atkinson & Millener 1991; Clout & Hay 1989), reduced to what has been called "the wreckage of an avifauna" (Diamond, 1984), as well as the introduction of a suite of mammalian predators of seeds and seedlings, opens plant recruitment to new challenges and opportunities for research (Atkinson and Cameron, 1993; Kelly et al., 2010).

The aim of this thesis was to understand the impacts of bird-mediated seed dispersal on the spatial patterns of seed deposition, and its possible consequences for plant recruitment in podocarp-broadleaved forests of New Zealand. I estimated indirectly the consequences of the reduction in the seed disperser assemblage as an increase in seed densities, and the consequences of the introduction of mammalian predators through exclosures protecting the seeds and seedlings of the attack from mammals. I studied these patterns in the context of tree seed size, as the disperser assemblages for the different tree species is partially determined by their seed sizes, leaving larger-seeded species with a reduced assemblage of dispersers. In this chapter I will synthesize the main results of my thesis, as well as highlight the questions that remain open for future research.

6.1 Importance of seed dispersal for the spatial patterns of seed deposition

Animal mediated seed dispersal in New Zealand forests mainly involves birds (Clout and Hay, 1989; Kelly et al., 2010), and occasionally introduced mammals as the brushtail possum (Williams et al., 2000; Dungan and Norton, 2003; Williams, 2003) and feral pigs (O'Connor & Kelly in press). The separation of birds and possums as dispersal agents is difficult with my sampling methods; however, as I found no possum faeces in my seed traps I consider my results to mainly reflect bird-mediated seed dispersal.

6.1.1 **Effects on seed diversity**

Seed diversity at ground level increased through seed dispersal (Chapter 2). This increase implies the potential to increase plant diversity at local level, if seed dispersal patterns are maintained through

seedling survival and recruitment. However, the lack of information on the consequences of multispecific seed rain on species-specific seed and seedling survival makes it difficult to hypothesize the possible outcomes to the seedling, sapling and adult tree stages of this interaction. The increase in seed diversity was not linked to the basal areas of trees, classified according to their dispersal syndrome (all trees, fleshy-fruited trees or wind-dispersed trees) or dominant species. The spatial association between *D. cupressinum* (the dominant tree species) seeds and adults is maintained through seed dispersal; however, as we used non-dispersed (whole fruits) seeds to estimate the "absence of dispersers" situation, the actual numbers of fruits falling beneath the parent trees should be higher. Therefore, it is possible that I underestimated spatial association between non-dispersed seeds and trees. I also found evidence for seed transfer of *D. cupressinum* (a conifer) to heterospecific canopies (heterospecific seed transfer), particularly towards angiosperms in the plots. This result gives a possible starting point for a pattern previously described in New Zealand, where seedlings from podocarps have been observed recruiting associated to angiosperm trees (Beveridge, 1973; Norton, 1991; Lusk and Ogden, 1992). However, the mechanisms for the biased seed rain of podocarp seeds towards angiosperms still remain unknown. The spatial changes in seed deposition patterns I found can have important consequences for plant recruitment, as new microsites are reached through seed dispersal (e.g. *D. cupressinum* seeds under heterospecific trees) and new combinations of seeds on the ground will affect the survival probability of each individual seed in the group. In general, from the viewpoint of an individual plant, for its seeds to be not all underneath its own canopy (in competition with siblings) and not all underneath conspecifics (in competition with conspecific seedlings) would be expected to improve its number of surviving offspring (fitness).

6.1.2 **Effects on seed rain heterogeneity**

The heterogeneity present in the canopy of the forest was modified through seed dispersal, increasing the similarity between seed traps through the activity of the frugivores (Chapter 3). However, the relative contribution of the different species (*D. cupressinum*, *D. dacrydioides*, *P. taxifolia*, *E. dentatus*, *P. ferruginea* and *B. tawa*) to this change in the seed community was not the same. Some species (e.g. *D. cupressinum*) acted mainly as seed exporters to heterospecific canopies, having relatively low conspecific seed rain under its own canopy. Other species maintained a strong association between its canopy and its seeds, but also received seeds from heterospecific canopies, acting as seed importers in the forest (*D. dacrydioides*, *B. tawa*). This shows that frugivore activity in this forest is species-specific, not necessarily treating all canopy trees equally or predicted by the fruit size conditioning the dispersal assemblage. Species with similar potential dispersers can present different rates of fruit removal and seed deposition under its canopies (e.g. *E. dentatus* versus *B. tawa*). The nutritional contents of the fruit, the neighborhood surrounding the trees, as well as structural characteristics of the trees will interact to determine seed arrival and seed removal rates (Carlo, 2005; García et al., 2010; Blendinger et al., 2011). However, I did find some similarities

between the seed rain under the canopy of *B. tawa* and *P. ferruginea*, both species dispersed mainly by the New Zealand pigeon. The results of Chapter 3 also highlight indirectly the importance of filters acting post seed dispersal. The heterogeneity of the environment, biotic as much as abiotic, will determine differences in the survival of the seeds, depending on their specific requirements for regeneration and survival (Cavallero et al. in press; Grubb, 1977). The fate of seeds and seedlings in multi-specific clumps under the canopy of fleshy fruited trees is barely understood, especially in temperate forests.

6.2 Density-dependent mortality in New Zealand temperate forests

The effects of seed density on seed and seedling survival were species-specific, as previously described in the literature (Willson and Whelan, 1990; Hulme and Borelli, 1999; Alcántara et al., 2000). Seed size was not a relevant predictor for germination and seedling survival, although it was related to the strength of seed density effects on seed predation and to seed predation rate itself.

6.2.1 Seed and seedling predators

Exclusion of mammals through the use of cages in seed predation, seed germination and seedling survival experiments was the most important and constant (across developmental stages) predictor for propagule losses. Larger seeds suffered from increased seed predation from rats and possums (Chapter 4), and the larger the seed, the stronger the effect of seed density on seed predation rates. Similar relationships between seed predation risk and seed size have been previously described for another broadleaved-podocarp forest (Berry, 2006). In his study video recordings of seed predation events proved rodents and mammals as the main agents responsible for seed predation, and that possums are also targeting seeds already dispersed, on the ground (Berry, 2006). Seed predation rates for New Zealand trees were reported to be low in one study (Moles and Drake, 1999), however it was in a modified forest within an urban area, and left the seeds exposed for only a short time. Densities of the predators and of alternative foods both vary between sites, and also the methods used in the different studies will probably alter the overall attraction of predators to depots.

Beilschmiedia tawa presents a particular case of seed predation, where many seeds were eaten by the larvae of the native moth *Cryptaspasma querula* (Tortricidae). This insect also predates the seeds of another species in the same genus (*B. tarairi*), and in other genera (Wotton, 2007). Its impacts on seed survival inside cages have been found to be up to 30% of *Beilschmiedia tarairi* seeds in Wotton and Kelly (2011) and 67% of *B. tawa* in my study (Chapter 5). The effect of the reduction of feeding resources (seeds) for this native insect through seed predation by rodents and possums are far from understood, as well as what determines differential rates of seed losses to insect predation between years (Kelly et al., 2010).

6.2.2 **Distance from conspecifics**

Recruitment of the two species tested in my thesis for the presence of Janzen-Connell effects increased away from conspecifics, either by the effects of host-specific invertebrates and introduced mammals (*B. tawa*) or mammals only (*D. dacrydioides*) (Chapter 5). My study did not test specifically for the effects of soil pathogens or allelopathy on increased mortality under conspecifics, however I observed some seedling mortality on both species with no evident reason. Although this happened in the field and in the controlled experiment in the glasshouses, the causes are not known and further experiments to identify the exact causative agents of increased mortality under the parents would be very valuable.

In Chapter 5 I found that rodents and possums, despite being generalist predators which were expected to behave as density-responsive agents to resources in the environment, can behave as distance-responsive agents (Janzen, 1971). Seed and seedling mortality caused by these agents was increased under conspecific canopies, suggesting that rodents and possums can identify sources of seeds in the forest at ground level. The presence of Janzen-Connell effects in New Zealand forests has been found in all the species studied to date: *Beilschmiedia tarairi*, *B. tawa*, *Corynocarpus laevigatus*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum* and *Nothofagus solandrii* var. *cliffortioides* (Wilson et al. 2007; Wotton & Kelly 2011; this thesis). These species are all trees endemic to New Zealand, and belong to a variety of plant families including angiosperms and gymnosperms. Therefore Janzen-Connell effects are stronger than previously expected and may be very widespread in New Zealand. Although research has been biased towards animal-dispersed species (all the above except *Nothofagus*), the introduced mammals acting as seed/seedling predators can act as distance responsive species (chapter 5), and species-specific parasites and soil pathogens can also exist for wind-dispersed species, so I find no reason to expect a different result from the one found for the animal-dispersed species.

There has been relatively little research testing for Janzen-Connell effects in temperate compared to tropical forests, and the few studies are biased towards deciduous temperate forests in the Northern hemisphere (Carson et al. 2008; chapter 5). Evidence from the Northern hemisphere suggests that these effects are frequently present in temperate tree species, which is similar to the New Zealand situation. I know of no studies in the Southern Hemisphere beyond those already mentioned from New Zealand. The presence of Janzen-Connell effects on tree species in islands where mammalian pests were never introduced, and the comparison against sites where introduced mammals have been present would give us an idea of the real effects of mammals on plant recruitment in New Zealand forests. Clearly, there is a need for more research of Janzen-Connell effects in temperate evergreen forests of the Southern hemisphere, some of which are relatively diverse, and might also be affected by density-dependent processes.

6.3 Effects of rodents and possums on plant recruitment

Plenty of research in New Zealand has focused on the effects of ungulates, particularly red deer, on plant recruitment (Allen, Payton, & Knowlton, 1984; Bee et al., 2009; Bellingham & Allan, 2003; Wilson, Ruscoe, Burrows, McElrea, & Choquenot, 2006; among others). However, the effects of rodents and possums as seed and seedling predators have been studied less often (Moles and Drake, 1999; Wilson et al., 2003, 2007; Ruscoe et al., 2004; Berry, 2006). Most of these studies have found significant reductions in plant survival from the action of rodents, possums or both (Wilson et al., 2003, 2007; Ruscoe et al., 2004; Berry, 2006), confirming the importance of these agents in the modification of New Zealand's natural landscape. Large-seeded species were often found to be more at risk of seed predation by these introduced mammals (Berry 2006; Wotton & Kelly 2011, Chapter 4), however, there is also evidence for strong seed predation on medium and even small-seeded species in New Zealand forests (particularly "masting" species such as *Nothofagus* spp and *D. cupressinum*: McQueen & Lawrence 2008; Ruscoe et al. 2004, 2005; Wilson et al. 2007; Chapters 4 and 5). Manipulative experiments adding seedlings of different species at different densities, in sites with known pest densities, controlling for possum and rat access and monitoring the survival over time would give more detailed information about the impact of these groups on seedling mortality. Seed and seedling mortality are also affected by the background resources and the neighborhood where they are found (Celis-Diez et al., 2004; Bee et al., 2009), and rodents and possums have been shown to have certain preferences for what they consume (Beveridge, 1964; Beveridge and Daniel, 1965; Knowles and Beveridge, 1982). However, as studies on rat and possum diet are often based on analysis of stomach contents, the precise identification (species) of plant material can be difficult (Daniel, 1973; Sweetapple and Nugent, 1998), differentiation of plant material and coming from adults versus seedlings is almost impossible (Wilson et al., 2003).

6.4 Future research

Multiple questions have arisen during the development of this thesis. I consider that making them explicit can throw some light on the areas in need of research. I expect this section might help someone at the beginning of an extensive research project (like a Masters or a PhD student) finding some interesting gaps to fill in the ecological research on seed dispersal in New Zealand forests.

6.4.1 **Masting species**

Species with masting behaviour are unusually frequent in New Zealand ecosystems (Norton and Kelly, 1988; Webb and Kelly, 1993; Schauber et al., 2002). Research on mechanisms that could explain this behaviour is abundant (Burns 2012; Kelly & Sork 2002; Norton & Kelly 1988; Schauber et al. 2002, among others), and recently, new research regarding the consequences of masting on the populations of introduced mammals is available (Ruscoe et al., 2004, 2005; Harper, 2005; McQueen

and Lawrence, 2008). Surprisingly, the effects of masting on bird foraging behaviour and the spatial patterns of seed fall mediated by dispersers have received little or no attention in New Zealand ecosystems. It is possible that the spatial patterns of seed deposition I found in my thesis (Chapters 2 and 3) change or disappear in years of high fruit production of one or more of the dominant species. For example, seed dispersal patterns of *D. cupressinum* biased towards the angiosperms might disappear in a high production year, with extremely high seed fall under conspecifics (due to "frugivore" satiation, Hampe 2008) and relatively low under angiosperms. It is also possible that seed dispersers would concentrate on feeding on *D. cupressinum* trees, and would move its seeds more frequently through the landscape, generating instead a homogeneous layer of *D. cupressinum* seeds on the forest floor, independent of the identity of the trees and canopies above.

In Chapter 5 I found increased seed survival of *D. dacrydioides* away from the canopy of conspecifics, and increased seedling survival away from conspecifics when seedlings were in high densities. *Dacrycarpus dacrydioides* trees are scattered in Blue Duck Reserve, where the experiment was carried out. In a year of high fruit production I would expect to find high seed densities evenly distributed across the forest floor, seed predation by introduced mammals would also be equally distributed through the forest, and predators would likely to become satiated (Kelly and Sork, 2002), reducing the negative effects of conspecifics on survival.

6.4.2 **Neighborhood**

In chapter 3 I found that the different tree species had different seed arrival and seed removal rates; however, the mechanisms causing these different patterns are not clear yet. *Dacrycarpus dacrydioides*, the species with the largest fruit crop, was also was the species with the largest number of dispersed seeds. However, fruit crop size is not the only important variable in predicting fruit removal, as the fruiting neighborhood is also expected to increase fruit removal rates (Takahashi and Kamitani, 2004; Carlo, 2005; Carlo and Morales, 2008). It has been shown that the presence of conspecific neighbors can reduce removal rates at the tree scale, but the presence of heterospecific fruiting trees would increase frugivore visits, increasing fruit removal rates for the focal tree and the arrival of heterospecific seeds (Saracco et al., 2004, 2005; Carlo and Morales, 2008; Blendinger et al., 2011). It is possible that species that are more aggregated in the landscape receive heterospecific seeds less frequently, and that species scattered between other fruit-bearing species could act as strong seed importers in the community. Spatial mapping of the identity and distribution of the trees in my study site, as well as the characterization of the canopy architecture of the different species studied would help to elucidate the results presented here.

6.4.3 **Secondary seed dispersal**

Seed predation studies often assume that secondary seed dispersal (e.g. by scatter hoarding animals) does not exist for any plant species in New Zealand forests (e.g. Wilson et al. 2007; Wotton & Kelly 2011). This is supported in that the majority of the species do not form seed banks as their seeds are short-lived (Burrows, 1994). However, Rowarth et al. (2007) describe the characteristics of all seeds in New Zealand whose germination and survival in seed banks had been studied to that time, and stresses the need for more research in this area. Seeds from species like *P. ferruginea* and *Elaeocarpus* spp. present thick and hard seed coats, which require some time for rodents to chew through to access the endocarp. Intact seeds from these species are sometimes moved to sheltered microsites, where rats can eat through the seed coat safely. Their seeds have been observed in the trunks of standing tree ferns, and even seedlings of *Elaeocarpus dentatus* were observed in one of these microsites (S. Richardson, pers. comm.). However, no studies on this have been carried out to my knowledge. A recent article by O'Connor and Kelly (in press) shows how feral pigs eat and crush many seeds from fallen fruits of *Prumnopitys taxifolia* but disperse a minority intact; these seeds also have a thick seed coat, that can resist the gut passage through pigs. Germination of intact seeds (n = over 450 seeds) found in faeces collected in the field gave 68% germination, and although only 14% of the seeds fed to pigs in captivity were defecated intact, and 57% germinated, these numbers can still be significant for plant dispersal to new habitats .

Most of the seed predators in pre-human New Zealand are thought to be invertebrates, plus some bird species including ground foragers (Atkinson and Millener, 1991; Wilson, 2004; Duthie et al., 2006). Seed dispersal relied mainly on birds (Clout and Hay, 1989; Holdaway, 1989; Atkinson and Millener, 1991), two bats (one of them now extinct, and the other with very restricted distribution) (Wilson, 2004; King, 2005) and lizards (many of them extinct or reduced in density in the main islands) (Whitaker, 1987; Wotton, 2002). Today, seed dispersal function still relies mainly on birds, but with the inclusion of some exotic and self-introduced species, and a reduced number of the original species (Atkinson and Cameron, 1993; Kelly et al., 2006, 2010). The contribution of exotic mammals to seed dispersal is still insufficiently explored (except for possums: Dungan et al. 2002; Dungan & Norton 2003; Williams et al. 2000; Williams 2003; and one article on feral pigs O'Connor & Kelly in press). Information on current post-dispersal seed predation by native animals (vertebrates and invertebrates) is scarce, but it is known that the red-crowned parakeet (*Cyanoramphus novaezelandiae novaezelandiae*, currently present in offshore islands and uncommon in the mainland, Greene 1998) and weta (multiple species, Beveridge 1964; Duthie et al. 2006; Mirams 1957) forage on the forest floor. Pre-dispersal seed predation in forests has been relatively more studied than post-dispersal in the context of the native possible predators (Beveridge, 1964; Sullivan et al., 1995). Introduced mammalian seed and seedling predators are thought to be reducing drastically the present number of propagules (Berry, 2006), however, with the reduced information

regarding pre human New Zealand it is difficult to know if these new agents are causing more damage than was caused by native animals in pre-human New Zealand. The long-term persistence and species composition of the remaining New Zealand forests is uncertain, however, research like that presented in this thesis can inform models that may help to answer these urgent conservation issues.

7 References

Alcántara, J.M., Rey, P.J., Sánchez-Lafuente, A.M., Valera, F., 2000. Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. Oikos 88, 362-370.

Allan, H., 1961. Flora of New Zealand I: Indigenous Tracheophyta: Psilopsida, Lycopsida, Filicopsida, Gymnospermae, Dicotyledones. Government printer, Wellington.

Allen, R.B., Payton, I.J., Knowlton, J., 1984. Effects of ungulates on structure and species composition in the Urewera Forests as shown by exclosures. New Zealand Journal of Ecology 7, 119–130.

Alvarez-Loayza, P., Terborgh, J.W., 2011. Fates of seedling carpets in an Amazonian floodplain forest: intra-cohort competition or attack by enemies? Journal of Ecology 99, 1045-1054.

Anderson, D.R., 2008. Model based inferences in the life sciences: A primer on evidence. Springer, New York, New York, USA.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32–46.

Anderson, S.H., Kelly, D., Robertson, A.W., Ladley, J.J., Innes, J.G., 2006. Birds as pollinators and dispersers: a case study from New Zealand. Acta Zoologica Sinica 52, 112-115.

Aravena, J.C., Carmona, M.R., Pérez, C.A., Armesto, J.J., 2002. Changes in tree species richness, stand structure and soil properties in a successional chronosequence in northern Chiloé Island, Chile. Revista Chilena de Historia Natural 75, 339–360.

Arévalo, J., Delgado, J., Fernández-Palacios, J., 2007. Variation in fleshy fruit fall composition in an island laurel forest of the Canary Islands. Acta Oecologica 32, 152-160.

Atkinson, I.A.E., Cameron, E.K., 1993. Human influence on the terrestrial biota and biotic communities of New Zealand. Trends in Ecology & Evolution 8, 447-451.

Atkinson, I.A.E., Millener, P.R., 1991. An ornithological glimpse into New Zealand's pre-human past. Acta XX Congressus Internationalis Ornithologici 1, 129-192.

Aukema, J.E., Martínez del Rio, C., 2002. Variation in mistletoe seed deposition: effects of intra-and interspecific host characteristics. Ecography 25, 139–144.

Barton, K., 2012. MuMIn: Multi-model inference. R package, version 0.12.2. Available at: http://r-forge.r-project.org/pro- jects/mumin/.

Bates, D.B., Maechler, M., Bolker, B.M., 2011. lme4: Linear mixed-effects models using S4 classes. R package, version 0.999375-42. Available at: http://CRAN.R-project.org/package=lme4.

Beckman, N.G., Neuhauser, C., Muller-Landau, H.C., 2012. The interacting effects of clumped seed dispersal and distance- and density-dependent mortality on seedling recruitment patterns. Journal of Ecology 100,862-873.

Bee, J.N., Tanentzap, A.J., Lee, W.G., Lavers, R.B., Mark, A.F., Mills, J.A., Coomes, D.A., 2009. The benefits of being in a bad neighbourhood: plant community composition influences red deer foraging decisions. Oikos 118, 18-24.

Bell, R., 1996. Seed dispersal by kereru (*Hemiphaga novaeseelandiae*) at Wenderholm Regional Park. MSc thesis, University of Auckland, Auckland, New Zealand.

Bellingham, P.J., Allan, C.N., 2003. Forest regeneration and the influences of white-tailed deer (*Odocoileus virginianus*) in cool temperate New Zealand rain forests. Forest Ecology and Management 175, 71-86.

Bellingham, P.J., Wiser, S.K., Wright, A.E., Cameron, E.K., Forester, L.J., 2010. Disperser communities and legacies of goat grazing determine forest succession on the remote Three Kings Islands, New Zealand. Biological Conservation 143, 926-938.

Berry, C.J.J., 2006. Post-dispersal seed predation in a conifer-broadleaf forest remnant: the importance of exotic mammals. PhD thesis, Lincoln University, Lincoln, New Zealand.

Beveridge, A., 1964. Dispersal and destruction of seed in central North Island Podocarp forests. Proceedings of the New Zealand Ecological Society 11, 48-56.

Beveridge, A., 1973. Regeneration of podocarps in a central North Island forest. New Zealand Journal of Forestry 18, 23–35.

Beveridge, A., Daniel, M.J., 1965. Observations on a high population of brown rats (*Rattus norvegicus* Berkenhout 1767) on Mokoia Island, Lake Rotorua. New Zealand Journal of Science 8, 174-189.

Blendinger, P.G., Blake, J.G., Loiselle, B., 2011. Composition and clumping of seeds deposited by frugivorous birds varies between forest microsites. Oikos 120, 463-471.

Blendinger, P.G., Villegas, M., 2010. Crop size is more important than neighborhood fruit availability for fruit removal of *Eugenia uniflora* (Myrtaceae) by bird seed dispersers. Plant Ecology 212, 889-899.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24, 127-35.

Breese, E.D., Timmins, S.M., Garrick, A.S., Owen, J.M., Jane, G.T., 1986. Kaikoura Ecological District. Wellington.

Bremner, A., Barratt, B., Butcher, C., Patterson, G., 1989. The effects of mammalian predation on invertebrate behaviour in South West Fiordland. New Zealand Entomologist 12, 72-75.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Verlag.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65, 23-35.

Burns, K., 2012. Masting in a temperate tree: Evidence for environmental prediction? Austral Ecology 37, 175-182.

Burns, K.C., in press. Are introduced birds unimportant mutualists? A case study of frugivory in European blackbirds (*Turdus merula*). New Zealand Journal of Ecology.

Burrows, C.J., 1994. The seeds always know best. New Zealand Journal of Botany 32, 349–363.

Burrows, C.J., 2001. New Zealand seed ecology 5. Germination behaviour of the tree species *Dacrycarpus dacrydioides*, *Podocarpus totara*, *Prumnopitys ferruginea* and *P. taxifolia* (Gymnospermae: Podocarpaceae). Rebus publications, Christchurch.

Cadotte, M.W., 2006. Dispersal and Species Diversity: A Meta-Analysis. The American Naturalist 168, 913-924.

Campbell, D., 1978. The effects of rats on vegetation, in: Dingwall, P., Atkinson, I.A.E., Hay, C. (Eds.), The Ecology and Control of Rodents in New Zealand Nature Reserves. Department of Lands and Survey Information Series #4, pp. 99-120.

Carlo, T.A., 2005. Interspecific neighbors change seed dispersal pattern of an avian-dispersed plant. Ecology 86, 2440-2449.

Carlo, T.A., Aukema, J.E., Morales, J.M., 2007. Plant–frugivore interactions as spatially explicit networks: integrating frugivore foraging with fruiting plant spatial patterns, in: Dennis, A.J., Schupp, E., Green, R., Westcott, D. (Eds.), Seed Dispersal: Theory and Its Application in a Changing World. CAB International Publishing, Wallingford, UK, pp. 369-390.

Carlo, T.A., Morales, J.M., 2008. Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. Journal of Ecology 96, 609–618.

Carson, W.P., Anderson, J., Leight Jr, E., Schnitzer, S., 2008. Challenges associated with testing and falsifying the Janzen-Connell hypothesis: a review and critique, in: Carson, W.P., Schnitzer, S. (Eds.), Tropical Forest Community Ecology. Wiley-Blackwell, Hoboken, pp. 210-241.

Cavallero, L., Aizen, M., Raffaele, E., in press. Endozoochory decreases environmental filtering imposed to seedlings. Journal of Vegetation Science.

Celis-Diez, J.L., Bustamante, R.O., Vásquez, R.A., 2004. Assessing frequency-dependent seed size selection: a field experiment. Biological Journal of the Linnean Society 81, 307-312.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31, 343-366.

Clark, C.J., Poulsen, J.R., Bolker, B.M., Connor, E.F., Parker, V.T., 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. Ecology 86, 2684-2694.

Clark, C.J., Poulsen, J.R., Connor, E.F., Parker, V.T., 2004. Fruiting trees as dispersal foci in a semi-deciduous tropical forest. Oecologia 139, 66-75.

Clark, C.J., Poulsen, J.R., Levey, D.J., 2012. Vertebrate herbivory impacts seedling recruitment more than niche partitioning or density-dependent mortality. Ecology 93, 554-64.

Clark, J., Bell, D., Chu, C., Courbaud, B., Dietze, M., Hersh, M., HilleRisLambers, J., Ibáñez, I., LaDeau, S., McMahon, S.M., Metcalf, J., Mohan, J., Moran, E., Pangle, L., Pearson, S., Salk, C., Shen, Z., Valle, D., Wyckoff, P., 2010. High-dimensional coexistence based on individual variation: a synthesis of evidence. Ecological Monographs 80, 569-608.

Clout, M.N., Hay, J., 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. New Zealand Journal of Ecology 12, 27–33.

Clout, M.N., Karl, B.J., Gaze, P., 1991. Seasonal movements of New Zealand pigeons from a lowland forest reserve. Notornis 38, 37–47.

Clout, M.N., Karl, B.J., Pierce, R.J.R., Robertson, H.A., 1995. Breeding and survival of New Zealand pigeons *Hemiphaga novaeseelandiae*. Ibis 137, 264-271.

Clout, M.N., Tilley, J., 1992. Germination of miro (*Prumnopitys ferruginea*) seeds after consumption by New Zealand pigeons (*Hemiphaga novaeseelandiae*). New Zealand Journal of Botany 50, 25–28.

Connell, J., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees, in: den Boer, P., Gradwekk, G. (Eds.), Dynamics of Populations. Centre for Agricultural Publications and Documentation, Wageningen, The Netherlands, pp. 298-310.

Conrad, K., 2001. SadieShell. version 1.22. http://www.rothamsted.ac.uk/pie/sadie/SADIE_home_page_1.htm.

Coomes, D.A., 2003. Colonization, tolerance, competition and seed-size variation within functional groups. Trends in Ecology & Evolution 18, 283-291.

Coomes, D.A., Allen, R.B., Bentley, W. A., Burrows, L.E., Canham, C.D., Fagan, L., Forsyth, D.M., Gaxiola, A., Parfitt, R.L., Ruscoe, W.A., Wardle, D.A., Wilson, D.J., Wright, E.F., 2005. The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering. Journal of Ecology 93, 918-935.

Cottam, Y., 2010. Characteristics of green rimu fruit that might trigger breeding in kakapo. MSc thesis, Massey University, Palmerston North, New Zealand.

Cottam, Y., Merton, D., Hendriks, W., 2006. Nutrient composition of the diet of parent-raised kakapo nestlings. Notornis 53, 90-99.

Daniel, M.J., 1973. Seasonal diet of the ship rat (*Rattus r. rattus*) in lowland forest in New Zealand. Proceedings of the New Zealand Ecological Society 20, 21-30.

Daniel, M.J., 1976. Feeding by the short-tailed bat (*Mystacina tuberculata*) on fruit and possibly nectar. New Zealand Journal of Zoology 3, 391-398.

Das, A., Battles, J., van Mantgem, P.J., Stephenson, N.L., 2008. Spatial elements of mortality risk in old-growth forests. Ecology 89, 1744–1756.

Dawson, J., Lucas, R., 2011. New Zealand's native trees. Craig Potton Publishing, Nelson, New Zealand.

Debussche, M., Isenmann, P., 1994. Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. Oikos 69, 414–426.

Dennis, A.J., Westcott, D.A., 2007. Estimating dispersal kernels produced by a diverse community of vertebrates, in: Dennis, A.J., Green, R., Schupp, E.W., Westcott, D.A. (Eds.), Frugivory and Seed Dispersal: Theory and Applications in a Changing World. CAB International Publishing, Wallingford, UK, pp. 201-228.

Diamond, J., 1984. Distributions of New Zealand birds on real and virtual islands. New Zealand Journal of Ecology 7, 37-55.

Dijkgraaf, A.C., 2002. Phenology and frugivory of large-fruited species in northern New Zealand and the impacts of introduced mammals. PhD Thesis, University of Auckland, Auckland, New Zealand.

Dungan, R.J., Norton, D.A., 2003. Possums as seed dispersers in New Zealand: A response to Williams (2003). New Zealand Journal of Ecology 27, 225–226.

Dungan, R.J., O'Cain, M., Lopez, M., Norton, D.A., 2002. Contribution by possums to seed rain and subsequent seed germination in successional vegetation, Canterbury, New Zealand. New Zealand Journal of Ecology 26, 121-128.

Duthie, C., Gibbs, G., Burns, K.C., 2006. Seed dispersal by weta. Science 311, 1575.

Enright, N., Cameron, E.K., 1988. The soil seed bank of a kauri (*Agathis australis*) forest remnant near Auckland, New Zealand. New Zealand Journal of Botany 26, 223-236.

Flörchinger, M., Braun, J., Böhning-Gaese, K., Schaefer, H.M., 2010. Fruit size, crop mass, and plant height explain differential fruit choice of primates and birds. Oecologia 164, 151-61.

Forget, P.M., Dennis, A.J., Mazer, P.A., Jansen, P.A., Kitamura, S., Lambert, J.S., Westcott, D.A., 2007. Seed allometry and disperser assemblages in tropical rainforests: a comparison of four floras on different continents, in: Dennis, A.J., Green, R., Schupp, E.W., Westcott, D.A. (Eds.), Frugivory and Seed Dispersal: Theory and Applications in a Changing World. CAB International Publishing, Wallingford, UK, pp. 5-36.

García, D., 2001. Effects of seed dispersal on *Juniperus communis* recruitment on a Mediterranean mountain. Journal of Vegetation Science 12, 839–848.

García, D., Martínez, I., Obeso, J.R., 2007. Seed transfer among bird-dispersed trees and its consequences for post-dispersal seed fate. Basic and Applied Ecology 8, 533-543.

García, D., Obeso, J.R., Martínez, I., 2005. Rodent seed predation promotes differential recruitment among bird-dispersed trees in temperate secondary forests. Oecologia 144, 435–446.

García, D., Zamora, R., Amico, G.C., 2010. Birds as suppliers of seed dispersal in temperate ecosystems: Conservation guidelines from real-world landscapes. Conservation Biology 24, 2-5.

Gaxiola, A., Burrows, L.E., Coomes, D.A., 2008. Tree fern trunks facilitate seedling regeneration in a productive lowland temperate rain forest. Oecologia 155, 325-35.

Godoy, J., Jordano, P., 2001. Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. Molecular ecology 10, 2275-83.

Grant-Hoffman, M.N., Barboza, P.S., 2010. Herbivory in invasive rats: criteria for food selection. Biological Invasions 12, 805-825.

Grant-Hoffman, M.N., Mulder, C.P., Bellingham, P.J., 2010. Invasive rats alter woody seedling composition on seabird-dominated islands in New Zealand. Oecologia 163, 449-60.

Greene, D., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., Simard, M.-J., 1999. A review of the regeneration dynamics of North American boreal forest tree species. Canadian Journal of Forest Research 29, 824-839.

Greene, T., 1998. Foraging ecology of the red-crowned parakeet (*Cyanoramphus novaezelandiae novaezelandiae*) and yellow-crowned parakeet (*C. auriceps auriceps*) on Little Barrier Island, Hauraki Gulf, New Zealand. New Zealand Journal of Ecology 22, 161-171.

Grubb, P., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews 52, 107-145.

Hampe, A., 2008. Fruit tracking, frugivore satiation, and their consequences for seed dispersal. Oecologia 156, 137-45.

Hampe, A., García-Castaño, J.L., Schupp, E.W., Jordano, P., 2008. Spatio-temporal dynamics and local hotspots of initial recruitment in vertebrate-dispersed trees. Journal of Ecology 96, 668-678.

Harper, G.A., 2005. Heavy rimu (*Dacrydium cupressinum*) mast seeding and rat (*Rattus* spp.) population eruptions on Stewart Island/Rakiura. New Zealand Journal of Zoology 32, 155–162.

Hautier, Y., Saner, P., Philipson, C., Bagchi, R., Ong, R.C., Hector, A., 2010. Effects of seed predators of different body size on seed mortality in Bornean logged forest. PloS one 5, e11651.

Herrera, C.M., 2002. Seed dispersal by vertebrates, in: Herrera, C.M., Pellmyr, O. (Eds.), Plant–animal Interactions: An Evolutionary Approach. Blackwell Science, pp. 185-208.

Herrera, C.M., Jordano, P., Lopez-Soria, L., Amat, J.A., 1994. Recruitment of a mast-fruiting, bird-dispersed tree: Bridging frugivore activity and seedling establishment. Ecological Monographs 64, 315.

Herrera, J.M., Morales, J.M., García, D., 2011. Differential effects of fruit availability and habitat cover for frugivore-mediated seed dispersal in a heterogeneous landscape. Journal of Ecology 99, 1100-1107.

HilleRisLambers, J., Lambers, R., Clark, J.S., Beckage, B., Lambers, J.H.R., 2002. Density-dependent mortality and the latitudinal gradient in species diversity. Nature 417, 732-5.

Holdaway, R., 1989. New Zealand's pre-human avifauna and its vulnerability. New Zealand Journal of Ecology 12, 11–25.

Howe, H.F., 1989. Scatter-and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79, 417-426.

Howe, H.F., Miriti, M.N., 2004. When seed dispersal matters. BioScience 54, 651.

Howe, H.F., Smallwood, J., Henry, I., 1982. Ecology of Seed Dispersal. Annual Review of Ecology and Systematics 13, 201-228.

Hubbell, S.P., 1980. Seed predation and the coexistence of tree species in tropical forests. Oikos 35, 214.

Hulme, P.E., Borelli, T., 1999. Variability in post-dispersal seed predation in deciduous woodland: relative importance of location, seed species, burial and density. Plant Ecology 145, 149–156.

Hurst, S.E., Turnbull, M.H., Norton, D.A., 2002. The effect of plant light environment on mycorrhizal colonisation in field-grown seedlings of podocarp-angiosperm forest tree species. New Zealand Journal of Botany 40, 65-72.

Hyatt, L.A., Rosenberg, M.S., Howard, T.G., Bole, G., Fang, W., Anastasia, J., Brown, K., Grella, R., Hinman, K., Kurdziel, J.P., Gurevitch, J., 2003. The distance dependence prediction of the Janzen-Connell hypothesis: a meta-analysis. Oikos 103, 590-602.

Innes, J.G., 1979. Diet and reproduction of ship rats in the northern Tararuas. New Zealand Journal of Ecology 2, 85-86.

Innes, J.G., Kelly, D., Overton, J., Gillies, C., 2010. Predation and other factors currently limiting New Zealand forest birds. New Zealand Journal of Ecology 34, 86-114.

Innes, J.G., Nugent, G., Prime, K., Spurr, E.B., 2004. Responses of kukupa (*Hemiphaga novaeseelandiae*) and other birds to mammal pest control at Motatau , Northland. New Zealand Journal of Ecology 28, 73-81.

Izhaki, I., Walton, P.B., Safriel, U.N., 1991. Seed shadows generated by frugivorous birds in an Eastern Mediterranean scrub. The Journal of Ecology 79, 575.

James, I.L., Norton, D.A., 2002. Helicopter-based natural forest management for New Zealand's rimu (*Dacrydium cupressinum*, Podocarpaceae) forests. Forest Ecology and Management 155, 337–346.

Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist 104, 501-528.

Janzen, D.H., 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2, 465-492.

Jordano, P., García, C., Godoy, J., García-Castaño, J.L., 2007. Differential contribution of frugivores to complex seed dispersal patterns. Proceedings of the National Academy of Sciences of the United States of America 104, 3278-82.

Jordano, P., Schupp, E.W., 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. Ecological Monographs 70, 591-615.

Kelly, D., Ladley, J.J., Robertson, A.W., Anderson, S.H., Wotton, D.M., Wiser, S.K., 2010. Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit- dispersal in New Zealand. New Zealand Journal of Ecology 34, 66-85.

Kelly, D., Robertson, A.W., Ladley, J.J., Anderson, S.H., McKenzie, R., 2006. Relative (un) importance of introduced animals as pollinators and dispersers of native plants. Biological Invasions in New Zealand 186, 227–245.

Kelly, D., Sork, V.L., 2002. Mast seeding in perennial plants: Why, How, Where? Annual Review of Ecology and Systematics 33, 427-447.

King, C., 2005. The handbook of New Zealand Mammals, 2nd. Ed. ed. Oxford University Press.

Knowles, B., Beveridge, A., 1982. Biological flora of New Zealand 9. *Beilschmiedia tawa* (A. Cunn.) Benth. et Hook. F. ex Kirk (Lauraceae) Tawa. New Zealand Journal of Botany 20, 37–54.

Kwit, C., Levey, D.J., Greenberg, C.H., 2004. Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. Oikos 107, 303-308.

Kwit, C., Levey, D.J., Turner, S.A., Clark, C.J., Poulsen, J.R., 2007. Out of One Shadow and into Another: Causes and consequences of spatially contagious seed dispersal by frugivores, in: Dennis, A.J., Schupp, E.W., Green, R.J., Westcott, D.A. (Eds.), Seed Dispersal: Theory and Its Application in a Changing World. CAB International Publishing, Wallingford, UK, pp. 427-444.

Lázaro, A., Traveset, A., Castillo, A., 2006. Spatial concordance at a regional scale in the regeneration process of a circum-Mediterranean relict (*Buxus balearica*): connecting seed dispersal to seedling establishment. Ecography 29, 683-696.

Lázaro, A., Traveset, A., Méndez, M., 2006. Masting in *Buxus balearica*: assessing fruiting patterns and processes at a large spatial scale. Oikos 115, 229–240.

Levey, D.J., Martínez del Rio, C., 2001. It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. The Auk 118, 819-831.

Levey, D.J., Sargent, S., 2000. A simple method for tracking vertebrate-dispersed seeds. Ecology 81, 267.

Lin, Y.-C., Chang, L.-W., Yang, K.-C., Wang, H., Sun, I.-F., 2011. Point patterns of tree distribution determined by habitat heterogeneity and dispersal limitation. Oecologia 165, 175-84.

Lloyd, B.D., 2005. Lesser Short-tailed bat, in: King, C.M. (Ed.), The Handbook of New Zealand Mammals. Oxford University Press, Melbourne.

Lord, J.M., Markey, A.S., Marshall, J., 2002. Have frugivores influenced the evolution of fruit traits in New Zealand, in: Levey, D., Silva, W.R., Galetti, M. (Eds.), Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CAB International Wallingford, UK, pp. 55–68.

Lusk, C.H., Ogden, J., 1992. Age structure and dynamics of a Podocarp-Broadleaf forest in Tongariro National Park, New Zealand. The Journal of Ecology 80, 379.

Lusk, C.H., Smith, B., 1998. Life history differences and tree species coexistence in an old-growth New Zealand rain forest. Ecology 79, 795-806.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Science, Oxford, UK.

Mari, L., Casagrandi, R., Gatto, M., Avgar, T., Nathan, R., 2008. Movement strategies of seed predators as determinants of plant recruitment patterns. The American Naturalist 172, 694-711.

Martin, P.H., Canham, C.D., 2010. Dispersal and recruitment limitation in native versus exotic tree species: life-history strategies and Janzen-Connell effects. Oikos 119, 807-824.

Martínez, I., García, D., Obeso, J.R., 2008. Differential seed dispersal patterns generated by a common assemblage of vertebrate frugivores in three fleshy-fruited trees. Ecoscience 15, 189-199.

Mason, N.W.H., Peltzer, D.A., Richardson, S.J., Bellingham, P.J., Allen, R.B., 2010. Stand development moderates effects of ungulate exclusion on foliar traits in the forests of New Zealand. Journal of Ecology 98, 1422-1433.

Mazerolle, M., 2012. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package, version 1.24. Available at http://CRAN.R-project.org/package= AICcmodavg.

McCay, T.S., McCay, D.H., 2008. Processes regulating the invasion of European buckthorn (*Rhamnus cathartica*) in three habitats of the northeastern United States. Biological Invasions 11, 1835-1844.

McCune, B., Grace, J., 2002. Analysis of ecological communities. MjM Software Design, Oregon, United States of America.

McEwen, W.M., 1978. The food of the New Zealand pigeon (*Hemiphaga novaeseelandiae novaeseelandiae*). New Zealand Journal of Ecology 1, 99-108.

McQueen, S., Lawrence, B., 2008. Diet of ship rats following a mast event in beech (*Nothofagus* spp.) forest. New Zealand Journal of Ecology 32, 214–218.

Metcalfe, D., Grubb, P., 1997. The responses to shade of seedlings of very small-seeded tree and shrub species from tropical rain forest in Singapore. Functional Ecology 11, 215-221.

Mirams, R., 1957. Aspects of the natural regeneration of the Kauri (*Agathis australis* Salisb.). Transactions of the Royal Society of New Zealand 84, 661-680.

Moles, A.T., Drake, D.R., 1999. Post-dispersal seed predation on eleven large-seeded species from the New Zealand flora: a preliminary study in secondary forest. New Zealand Journal of Botany 37, 679–685.

Moles, A.T., Hodson, D., Webb, C.J., 2000. Seed size and shape and persistence in the soil in the New Zealand flora. Oikos 89, 541-545.

Moles, A.T., Warton, D.I., Westoby, M., 2003. Do small-seeded species have higher survival through seed predation than large-seeded species? Ecology 84, 3148-3161.

Moles, A.T., Westoby, M., 2003. Latitude, seed predation and seed mass. Journal of Biogeography 30, 105-128.

Morales, J.M., Carlo, T.A., 2006. The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. Ecology 87, 1489–1496.

Morgan-Richards, M., Trewick, S.A., Dunavan, S., 2008. When is it coevolution? The case of ground wētā and fleshy fruits in New Zealand. New Zealand Journal of Ecology 32, 108-112.

Muller-Landau, H.C., Wright, S.J., Calderón, O., Condit, R., Hubbell, S.P., 2008. Interspecific variation in primary seed dispersal in a tropical forest. Journal of Ecology 96, 653-667.

Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution 15, 278-285.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A., 2008. Mechanisms of long-distance seed dispersal. Trends in Ecology & Evolution 23, 638-47.

New Zealand Meteorological Service, 2012. New Zealand Meteorological Service. URL www.metservice.co.nz. Accessed on March 2012.

Norton, D.A., 1991. Seedling and sapling distribution patterns in a coastal podocarp forest, Hokitika Ecological District, New Zealand. New Zealand Journal of Botany 29, 463–466.

Norton, D.A., Courtney, S.P., 2000. Vegetation and flora of Blue Duck Scientific Reserve, Kaikoura. Canterbury Botanical Society Journal 34, 37-49.

Norton, D.A., Cochrane, C.H., Reay, S.D., 2005. Crown-stem dimension relationships in two New Zealand native forests. New Zealand Journal of Botany 43, 673–678.

Norton, D.A., Herbert, J., Beveridge, A., 1988. The ecology of *Dacrydium cupressinum*: A review. New Zealand Journal of Botany 26, 37–62.

Norton, D.A., Kelly, D., 1988. Mast Seeding Over 33 Years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: The Importance of Economies of Scale. Functional Ecology 2, 399.

Nugent, G., Fraser, W., Sweetapple, P., 2001. Top down or bottom up? Comparing the impacts of introduced arboreal possums and 'terrestrial' ruminants on native forests in New Zealand. Biological Conservation 99, 65-79.

Oksanen, J., 2011. Multivariate analysis of ecological communities in R: vegan tutorial. Available at http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf

Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R., Simpson, G., Solymos, P., Stevens, H., Wagner, H., 2011. vegan: Community Ecology Package. R package version 2.0-2. Available at http://CRAN.R-project.org/package=vegan

O'Connor, S., Kelly, D., in press. Seed dispersal of matai (*Prumnopitys taxifolia*) by feral pigs (*Sus scrofa*). New Zealand Journal of Ecology.

O'Donnell, C.F.J., Dilks, P., 1994. Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. New Zealand Journal of Ecology 18, 87–107.

Packer, A., Clay, K., 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. Nature 404, 278-81.

Perry, J.N., Dixon, P.M., 2002. A new method to measure spatial association for ecological count data. Ecoscience 9, 133–141.

Perry, J.N., Winder, L., Holland, J.M., Alston, R.D., 1999. Red-blue plots for detecting clusters in count data. Ecology Letters 2, 106-113.

Pickett, S., Collins, S., Armesto, J.J., 1987. Models, mechanisms and pathways of succession. The Botanical Review 53, 335-371.

Pinheiro, J.C., Bates, D.B., 2000. Mixed effects models in S and S-plus. Springer, New York.

Poulsen, J.R., Clark, C.J., Connor, E.F., Smith, T.B., 2002. Differential Resource Use By Primates and Hornbills: Implications for Seed Dispersal. Ecology 83, 228-240.

Powlesland, R.G., Moran, L.R., Wotton, D.M., 2011. Satellite tracking of kereru (*Hemiphaga novaeseelandiae*) in Southland, New Zealand: impacts, movements and home range. New Zealand Journal of Ecology 35, 229–235.

Pérez-Ramos, I.M., Marañón, T., 2011. Community-level seedling dynamics in Mediterranean forests: uncoupling between the canopy and the seedling layers. Journal of Vegetation Science 23, 526-540.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reid, B., Ordish, R., Harrison, M., 1982. An analysis of the gizzard contents of 50 North Island brown kiwis, *Apteryx australis mantelli*, and notes on feeding observations. New Zealand Journal of Ecology 5, 76-85.

Robertson, C., Hyvönen, P., Fraser, M., Pickard, C., 2007. Atlas of bird distribution in New Zealand 1999–2004. Ornithological Society of New Zealand, Wellington.

Rowarth, J., Hampton, J., Hill, M., 2007. New Zealand native seed germination requirements: a review. New Zealand Journal of Botany 45, 485–501.

Rufaut, C., Gibbs, G.W., 2003. Response of a tree weta population (*Hemideina crassidens*) after eradication of the Polynesian rat from a New Zealand island. Restoration Ecology 11, 13-19.

Ruscoe, W.A., Elkinton, J.S., Choquenot, D., Allen, R.B., 2005. Predation of beech seed by mice: effects of numerical and functional responses. Journal of Animal Ecology 74, 1005-1019.

Ruscoe, W.A., Wilson, D.J., McElrea, L.M., McElrea, G., Richardson, S.J., 2004. A house mouse (*Mus musculus*) population eruption in response to rimu (*Dacrydium cupressinum*) seedfall in southern New Zealand. New Zealand Journal of Ecology 28, 259–265.

Russo, S.E., Augspurger, C.K., 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecology Letters 7, 1058-1067.

Sallabanks, R., 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. Ecology 74, 1326-1336.

Salmon, J., 1980. The native trees of New Zealand. Reed, Wellington, New Zealand.

Saracco, J.F., Collazo, J., Groom, M.J., 2004. How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. Oecologia 139, 235-45.

Saracco, J.F., Collazo, J., Groom, M.J., 2005. Crop size and fruit neighborhood effects on bird visitation to fruiting *Schefflera morototoni* trees in Puerto Rico. Biotropica 37, 81-87.

Schauber, E.M., Kelly, D., Turchin, P., Simon, C., Lee, W.G., Allen, R.B., Payton, I.J., Wilson, P.R., Cowan, P.E., Brockie, R., 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. Ecology 83, 1214–1225.

Schupp, E.W., 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107/108, 15-29.

Schupp, E.W., 1995. Seed-seedling conflicts, habitat choice and patterns of plant recruitment. American Journal of Botany 82, 399-409.

Schupp, E.W., Fuentes, M., 1995. Spatial patterns of seed dispersal and the unification of plant-population ecology. Ecoscience 2, 267–275.

Schupp, E.W., Jordano, P., Gómez, J.M., 2010. Seed dispersal effectiveness revisited: a conceptual review. The New Phytologist 188, 333-53.

Schupp, E.W., Milleron, T., Russo, S.E., 2002. Dissemination limitation and the origin and maintenance of species-rich Tropical Forests, in: Levey, D.J., Silva, R., Galetti, M. (Eds.), Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CAB International Publishing, Wallingford, UK, pp. 19-34.

Seidler, T.G., Plotkin, J.B., 2006. Seed dispersal and spatial pattern in tropical trees. PLoS biology 4, 2132-3137.

Silvertown, J., 2004. Plant coexistence and the niche. Trends in Ecology & Evolution 19, 605-611.

Skaug, H., Fournier, D., Nielsen, A., Magnusson, A., Bolker, B.M., 2011. glmmADMB: Generalized Linear Mixed Models using AD Model Builder. R package, version 0.7.0. Available at http://glmmadmb.r-forge.r-project.org.

Slocum, M.G., Horvitz, C.C., 2000. Seed arrival under different genera of trees in a neotropical pasture. Plant Ecology 149, 51-62.

Spear, D., Chown, S.L., 2009. Non-indigenous ungulates as a threat to biodiversity. Journal of Zoology 279, 1-17.

Spiegel, O., Nathan, R., 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. Ecology Letters 10, 718-28.

Spurr, E.B., Warburton, B., Drew, K., 1992. Bird abundance in different-aged stands of rimu (*Dacrydium cupressinum*)-implications for coupe-logging. New Zealand Journal of Ecology 16, 109–109.

Stead, E., 1937. The Maori rat. Transactions of the Royal Society of New Zealand 66, 178-181.

Sullivan, J., Burrows, C.J., Dugdale, J., 1995. Insect predation of seeds of native New Zealand woody plants in some central South Island localities. New Zealand Journal of Botany 33, 355-364.

Suzuki, M., Miyashita, T., Kabaya, H., Ochiai, K., Asada, M., Kikvidze, Z., in press. Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests. Oikos.

Swamy, V., Terborgh, J.W., 2010. Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. Journal of Ecology 98, 1096-1107.

Sweetapple, P., 2003. Possum (*Trichosurus vulpecula*) diet in a mast and non-mast seed year in a New Zealand Nothofagus forest. New Zealand Journal of Ecology 27, 157–167.

Sweetapple, P., Fraser, K., Knightbridge, P., 2004. Diet and impacts of brushtail possum populations across an invasion front in South Westland, New Zealand. New Zealand Journal of Ecology 28, 19–33.

Sweetapple, P., Nugent, G., 1998. Comparison of two techniques for assessing possum (*Trichosurus vulpecula*) diet from stomach contents. New Zealand Journal of 22, 181-188.

Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65, 13-21.

Takahashi, K., Kamitani, T., 2004. Factors affecting seed rain beneath fleshy-fruited plants. Plant Ecology 174, 247-256.

Terborgh, J.W., 2012. Enemies maintain hyperdiverse tropical forests. The American Naturalist 179, 303-14.

Terborgh, J.W., Alvarez-Loayza, P., Dexter, K.G., Cornejo, F., Carrasco, C., 2011. Decomposing dispersal limitation: limits on fecundity or seed distribution? Journal of Ecology 99, 935-944.

Thorsen, M.J., Dickinson, K., Seddon, P.J., 2009. Seed dispersal systems in the New Zealand flora. Perspectives in Plant Ecology, Evolution and Systematics 11, 285-309.

Towns, D.R., Ballantine, W., 1993. Conservation and restoration of New Zealand Island ecosystems. Trends in Ecology & Evolution 8, 452-457.

Turnbull, M.H., Whitehead, D., Tissue, D.T., Schuster, W.S.F., Brown, K.J., Griffin, K.L., 2003. Scaling foliar respiration in two contrasting forest canopies. Functional Ecology 17, 101–114.

Van der Pijl, L., 1982. Principles of dispersal in higher plants. Springer, Berlin.

Veblen, T., Stewart, G.H., 1982. The effects of introduced wild animals on New Zealand forests. Annals of the Association of American Geographers 72, 372-397.

Wang, B., Chen, J., 2009. Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents. Ecology 90, 3023-3032.

Wang, B.C., Smith, T.B., 2002. Closing the seed dispersal loop. Trends in Ecology & Evolution 17, 379-386.

Warburton, B., Kingsford, S., Lewitt, D., Spurr, E.B., 1992. Plant species preferences of birds in lowland rimu (*Dacrydium cupressinum*) forest-implications for selective-logging. New Zealand Journal of Ecology 16, 119–119.

Wardle, D., Barker, G., Yeates, G., Bonner, K.I., Ghani, A., 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecological Monographs 71, 587-614.

Warton, D.I., Wright, S.T., Wang, Y., 2012. Distance-based multivariate analyses confound location and dispersion effects. Methods in Ecology and Evolution 3, 89–101.

Watts, C., Armstrong, D., Innes, J.G., Thronburrow, D., 2011. Dramatic increases in weta (Orthoptera) following mammal eradication on Maungatautari – evidence from pitfalls and tracking tunnels. New Zealand Journal of Ecology 35, 261-272.

Webb, C.J., Kelly, D., 1993. The reproductive biology of the New Zealand flora. Trends in Ecology & Evolution 8, 442-7.

Webb, C.J., Simpson, M.J.A., 2001. Seeds of New Zealand: Gymnosperms and Dicotyledons. Manuka Press, Christchurch, New Zealand.

Whittingham, M.J., Stephens, P.A., Bradbury, R.B., Freckleton, R.P., 2006. Why do we still use stepwise modelling in ecology and behaviour ? Journal of Animal Ecology 75, 1182–1189.

Whitaker, A., 1987. The roles of lizards in New Zealand plant reproductive strategies. New Zealand Journal of Botany 25, 315-328.

White, E., Vivian-Smith, G., 2011. Contagious dispersal of seeds of synchronously fruiting species beneath invasive and native fleshy-fruited trees. Austral Ecology 36, 195-202.

Whitehead, D., Hall, G.M.J., Walcroft, A.S., Brown, K.J., Landsberg, J., Tissue, D.T., Turnbull, M.H., Griffin, K.L., Schuster, W.S.F., Carswell, F.E., Trotter, C., James, I.L., Norton, D.A., 2002. Analysis of the growth of rimu (*Dacrydium cupressinum*) in South Westland, New Zealand, using process-based simulation models. International Journal of Biometeorology 46, 66-75.

Wiegand, T., Martínez, I., Huth, A., 2009. Recruitment in tropical tree species: revealing complex spatial patterns. The American Naturalist 174, E106-40.

Williams, P.A., 2003. Are possums important dispersers of large-seeded fruit? New Zealand Journal of Ecology 27, 221–223.

Williams, P.A., Karl, B.J., 1996. Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. New Zealand Journal of Ecology 20, 127–145.

Williams, P.A., Karl, B.J., Bannister, P., Lee, W.G., 2000. Small mammals as potential seed dispersers in New Zealand. Austral Ecology 25, 523-532.

Willson, M.F., 1991. Dispersal of seeds by frugivorous animals in temperate forests. Revista Chilena de Historia Natural 64, 537–554.

Willson, M.F., Traveset, A., 2000. The ecology of seed dispersal, in: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. CAB International Publishing, Wallingford, UK, pp. 85-110.

Willson, M.F., Whelan, C., 1990. Variation in postdispersal survival of vertebrate-dispersed seeds: Effects of density, habitat, location, season, and species. Oikos 57, 191-198.

Wilson, D.J., Lee, W.G., Webster, R.A., Allen, R.B., 2003. Effects of possums and rats on seedling establishment at two forest sites in New Zealand. New Zealand Journal of Ecology 27, 147–155.

Wilson, D.J., Ruscoe, W.A., Burrows, L.E., McElrea, L.M., Choquenot, D., 2006. An experimental study of the impacts of understorey forest vegetation and herbivory by red deer and rodents on seedling establishment and species composition in Waitutu Forest, New Zealand. New Zealand Journal of Ecology 30, 191–207.

Wilson, D.J., Wright, E.F., Canham, C.D., Ruscoe, W.A., 2007. Neighbourhood analyses of tree seed predation by introduced rodents in a New Zealand temperate rainforest. Ecography 30, 105–119.

Wilson, K., 2004. Flight of the huia: ecology and conservation of New Zealand's frogs, reptiles, birds and mammals. Canterbury University Press, Christchurch, New Zealand.

Winder, L., Alexander, C.J., Holland, J.M., Woolley, C., Perry, J.N., 2001. Modelling the dynamic spatio-temporal response of predators to transient prey patches in the field. Ecology Letters 4, 568-576.

Wotton, D.M., 2002. Effectiveness of the common gecko (*Hoplodactylus maculatus*) as a seed disperser on Mana Island, New Zealand. New Zealand Journal of Botany 40, 639–647.

Wotton, D.M., 2007. Consequences of dispersal failure: kereru and large seeds in New Zealand. Sciences-New York.

Wotton, D.M., Kelly, D., 2011. Frugivore loss limits recruitment of large-seeded trees. Proceedings of the Royal Society B: Biological Sciences 278, 3345-3354.

Wright, S.J., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130, 1-14.

Wyman, T.E., Trewick, S. a., Morgan-Richards, M., Noble, A.D.L., 2011. Mutualism or opportunism? Tree fuchsia (*Fuchsia excorticata*) and tree weta (Hemideina) interactions. Austral Ecology 36, 261-268.

Yamazaki, M., Iwamoto, S., Seiwa, K., 2009. Distance- and density-dependent seedling mortality caused by several diseases in eight tree species co-occurring in a temperate forest. Plant Ecology 201, 181-196.

Zeileis, A., Kleiber, C., Jackman, S., 2008. Regression models for count data in R. Journal of Statistical Software 27, 1-25.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extension in ecology with R. Springer.